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THE WORLD OF LIFE

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THE WORLD OF LIFE



A GENERAL BIOLOGY

Wolfgang F. Pauli
BRADFORD JUNIOR COLLEGE

UNDER THE EDITORSHIP OF
Bentley Glass
JOHNS HOPKINS UNIVERSITY

HOUGHTON MIFFLIN COMPANY
The Riverside Press • Cambridge
BOSTON • NEW YORK • CHICAGO • DALLAS • ATLANTA • SAN FRANCISCO

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CAMBRIDGE, MASSACHUSETTS
PRINTED IN THE U.S.A.

EDITOR'S INTRODUCTION

When all is said, evolution remains the great unifying principle of modern biology. Nevertheless, it has not been too fashionable in the past three decades to make it the central theme in elementary college courses in that subject, at least in the United States. Yet since 1927 the advances made in the scientific understanding of evolutionary processes have made it clearer than ever that the fundamental aspects of the biological sciences meet in the evolutionary process and are fully intelligible only in its light. Here meet, on the one hand, the genes and the patterns of development they control, the structures and the functions of organisms, and the very biochemistry and biophysics of life; and on the other, the broader relations of individuals to one another and to their mundane environment, their adaptations, and the competitive struggle between them.

Teachers of biology should therefore welcome such a textbook as this one, by so enthusiastic and gifted a writer as Professor Pauli. Here is a well-rounded story of life in its evolutionary setting, with none of the important aspects of biology slighted and with all of them illuminated by their relation to the theme of life through the ages. Nor is emphasis laid unduly on the past. The present is stressed, and a consideration of the future forms a fitting climax.

In the face of a superfluity of good college textbooks of biology, there would seem to be little need for another, unless it be truly original in character. Of Dr. Pauli's *The World of Life* it can be said without hesitation that — from its unusual and exhilarating treatment of the physical setting of life to the thought-provoking final chapter on the human problems of population growth and eugenics — it bears the stamp of originality.

BENTLEY GLASS

The Johns Hopkins University

P R E F A C E

THIS BOOK is designed to serve as an introduction to the entire wide field of general biology. It has long been my belief that such an introduction is desirable for all types of students, whether they wish to specialize in this field or not. I am also convinced that the course can be reformulated to make it more significant for those students, especially, who take it as part of their general education and at the same time more helpful for those who will major in the biological sciences. After several years of experimentation, I therefore fixed upon three major guideposts for the course, and for this book which developed from it.

The first of these hardly needs defense. All teachers agree that an introductory course should stimulate interest and should stress the scientific method and thinking behind a particular science. Whenever possible, the genesis of a fact or idea should be given rather than the mere fact or idea alone. The student should be encouraged to peer behind the scenes to see for himself how facts were obtained, so that he may judge their validity, thus sharpening his own critical sense, and at the same time may gain the feeling that he is participating in the genesis of the ideas he is studying. The question, Will this fact contribute to a better understanding of principles? has served constantly in choosing out of the great mass of available knowledge the material presented in this book.

The second objective, attracting and stimulating the student, requires careful consideration. In recent times there has too often been apparent a tendency to dilute or water down a course by oversimplification. I have constantly tried to steer a middle course between too-easy a popularization and undue stress on masses of fact. The international language of scientific terminology, which serves as an invaluable tool if judiciously and moderately applied, is used instead of inaccurate colloquialisms. But formidable technical terms and names have been used with due regard for the student's unfamiliarity with them, and the language and style have been kept simple and straightforward. Examples and illustrations have been chosen with an eye as much to their interest as to their aid in understanding principles and, with the cooperation of the publishers, the book has been supplied with a generous number of original or newly drawn figures and carefully chosen halftones. These features, together with the narrative appeal of the evolutionary organization, will make the book, it is hoped, attractive to students.

The third objective is fundamental to the first two. Biologists unanimously agree that the one unifying principle which underlies the whole field is that of evolution.

It appeared to me some years ago that the logical way to teach the course in general biology would be to use this principle as a guiding theme. Surprisingly enough, however, there were, and are, no modern textbooks written primarily from this point of view. An outline was therefore drafted in which the unifying core would be the evolutionary sequence of life.

Since the introduction of this experimental text in mimeographed form some ten years ago, student reaction in my classes has shown a marked increase in interest and curiosity. The present book represents an expansion of that original text. Obviously, the use of evolution as a unifying principle does not imply that science knows the answers to ultimate origins or purposes, or that it is necessarily concerned with them, since these are the domain of philosophy and theology. The narrative merely relates descriptively the known and probable interactions of matter and forces responsible for the living world we observe today.

In accordance with these principles, the book begins with a survey of the background for evolving life, with theories of the extent, nature, and development of the universe, and of the genesis and evolution of the planet Earth — the immediate scene of life. Since modern science rests upon observable facts, living organisms are viewed as physico-chemical mechanisms, whatever other qualities they may possess. Accordingly, those principles of physics and chemistry essential to some grasp of the nature of living things are briefly sketched. In the light of these principles, the discussions of protoplasm, the cell, and theories of the possible origin of life take on richer meaning.

The origin and evolution of significant advances in patterns of living are traced for both plants and animals, with emphasis on such milestones as the possible nature of the first forms of life; the evolution of cell units; the use of the resources of sunlight by green plants; the enormous mobility and activity of animal organisms made possible by animal nutrition, with its lavish squandering of commandeered plant energy; the introduction of sex, which ended hereditary isolation; the appearance of the colonial and multicellular habits, bringing that size and complexity necessary for some domination over the environment, but also bringing natural death; the origin and development of organs making for increased efficiency; the transition from water to land; the evolution of intelligence and cognition; and many others.

Following this excursion through the realm of life is a closer examination of the anatomical and physiological nature of the dominant species, man. In keeping with the general scheme, human anatomy is presented as the dynamic outcome of embryonic processes which reflect the evolutionary history of the species. This follows a brief but more than usually detailed sketch of primate evolution and of anthropology. Genetic concepts have been introduced at many points along the way, but a more

complete consideration of genetics is reserved as an introduction to the final chapter on eugenics and euthenics, which it is hoped will serve as a real climax to the book. Here the full force of many concepts developed earlier is brought to bear on the problem of man's future — and the conclusion emerges that for the first time in the history of life, the future of a species may be determined by the conscious acts of that very species itself.

While evolution is used throughout as the binding theme, the book is by no means a treatise on evolution, and two related themes are interwoven with it. One of these is the nature and place of man on the planet; the other is the interdependence of all living things. Since the book is written for human beings, the story of evolution is in a compelling sense the story of man, and every opportunity has been taken to evaluate each step in evolution as a way-station of human history. Not only is the interdependence of living organisms in the web of life stressed, but the practical application of such knowledge is made to modern agriculture, to the problem of soil resources, and to the increasing problem of feeding the world population.

The main pedagogical question involved in adopting evolution as the organizing theme for a biology course or book is this: Does this organization give sufficient emphasis to the fundamental processes of life, an understanding of which is crucially important for the student? Pains have been taken to see that such topics as respiration, reproduction, transport, sensitivity, and so on, have been adequately discussed. Because these processes are discussed in terms of their development, as evolving themes running from the simplest organisms to the most complex, and in integral relation with the other parts of whole organisms, they gain greatly in significance since the student comes to see them as the dynamic and changing things they are. This at least has been my experience in using this organization in teaching.

Finally, I wish to acknowledge my gratitude to those who have made the writing of this book possible: to my wife and my two daughters for their unceasing help and understanding; to the successive classes of students whose interest and intellectual curiosity has enforced my belief in this method of presentation; to Dr. Bentley Glass of the Johns Hopkins University for the many constructive criticisms he has so generously volunteered; Dr. Edward S. Castle of Harvard University, and Dr. A. B. Novikoff of the University of Vermont, for their invaluable editorial assistance; to Dr. Alfred S. Romer of Harvard University; and to Mr. Elmer Smith, who has not only contributed his skill as an artist but has shown constant interest as a biologist in the development of the book.

WOLFGANG F. PAULI

BRADFORD, MASSACHUSETTS

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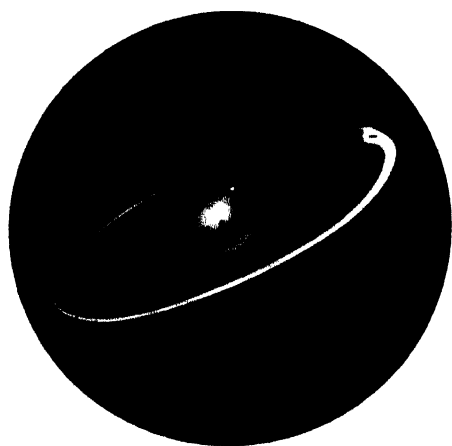
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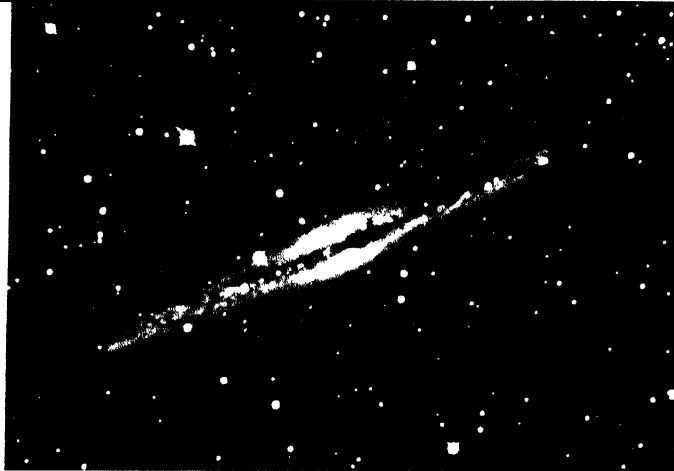
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PART ONE

BACKGROUNDS: THE PHYSICAL WORLD





The universe itself is the background of life. Our earth is but an invisible speck in a vast, disk-shaped cluster of stars, the Milky Way, which stretches for 100,000 light years through space, much like this giant nebula in Andromeda, here seen edge-on.

The Universe: The Frame of Life

Man is a part of life and therefore finds it difficult to view life with perspective. Its very closeness hides its extent in time, as the leaf before the eye may hide the tree. Life is a thing of many threads woven into the fabric of the universe. Hence to see it whole, and in relation to its setting, we shall begin, in these first chapters, with a sketch of the background out of which it came and the fundamental laws which govern it.

For the forming of life did not begin when life began. The beginning of life was but one step in a prodigiously long evolution. In the broadest sense, the creation of life began with the creation of the universe, of which it is a part. In one sense the story of life is the story of the universe, just as the story of the universe, at least for us, is the story of life. Much of the discussion in these pages will be an explanation of this statement.

What Science Is

Certain habits of thought characterize the man of science and give him the power of tracing truth, which to a degree sets him apart from the untrained observer. The modern man of science appears to make this seemingly familiar universe completely unfamiliar and virtually incomprehensible. Actually, of course, this only appears to be so. What he really does is to unearth facts generally overlooked; and then it turns out that these are beyond ultimate understanding by the human mind. But this should not be discouraging; for it will be at least a step toward the only thing we are capable of, that is, an *approach* to the truth.

The terrific power inherent in the "scientific" habit of thought need hardly be stressed

in this day and age. Yet, essentially, science is merely a habit of thought; it is the disciplined gathering and systematic recording of observed fact with reference to the discovery of generalized truths and general laws. Nothing must be taken for granted. Final recourse is always to observed facts, and acceptable theories are those which are based only upon facts and which conflict with as few facts as possible. It seems well nigh incredible that adherence to this simple formula should have achieved so much.

Men have lived so long in this particular corner of the universe that they come to take it more or less for granted. Perhaps the reader has retained or recaptured that sense of wonder and awe that is the birthright of all children. If not, it may be worth a determined effort to regain it, for odd as it may seem, this is a quality closely allied to the curiosity which motivates the scientist. Child-like wonder and questioning should not be confused with childishness. The imperturbability of pseudo-sophistication is a mark of the unthinking mind. Explorers tell that the savage is capable of wonder and admiration before the marvel of a lighted match, but that the marvel of an airplane is too far beyond his grasp, so that he automatically places it in the category of natural phenomena, such as thunder and lightning. Ignorant of the thousands of man-years of research in mechanics, aerodynamics, electricity, thermodynamics, electronics, chemistry, and subsidiary fields that made the plane possible, he explains the phenomenon quite simply: it flies because it is endowed with the spirit of flight.

We, of course, reject this explanation. Yet we may have our own pet "spirits," such as

gravity, electricity, or heat. That is, we may be satisfied with the statement that bodies attract each other and may accept a name for that fact, the name "gravity," and feel that we have learned something worth while. It is obvious, of course, that giving the thing a name does not explain it.

Today men of genius such as Einstein, Planck, Bohr, and others have made heroic efforts to exorcise these subjective "spirits." In order to reveal the realities beneath the visible world, they have attempted to strip it of the illusions with which it is commonly clothed. Slowly the great masses of humanity learn to follow where the few pioneer thinkers have pointed out the way, and slowly mankind moves toward the light of greater understanding. It would appear to be the duty of each individual to do his utmost to contribute toward this goal.

Why Study Science

Before beginning our journey into the world of life, we should agree upon our purpose. The universe is, in a sense, man's heritage. Whether he wishes it so or not, he has inherited the earth with all that is on it. It is not the earth as it first existed, but as it has been modified by generations that went before. Modern man has inherited his body and his mind. These too have undergone change upon change as generations followed generations. He will pass on this heritage to generations following, and it will be changed again. Whether this change will be for the better or worse lies in man to decide. This heritage brings with it privileges, for which we are indebted to generations past. It also brings responsibilities to generations yet unborn. It is not granted us to understand why this is so or even whether there is a basic purpose in it. Each man in his lifetime subscribes to a creed which he or someone else has formulated and which conforms to his own needs and temperament. We are the heirs and trustees of this heritage. The value of our contribution to it may be decided by the worth of the life philosophy we establish for ourselves. Dare we tackle such a task with-

out some knowledge of our legacy? This, then, is the larger purpose in studying biology: to approach reality as nearly as possible, so that through knowledge we may improve our contribution.

How Can Reality Be Known?

It is very difficult to approach reality. It is reasonable to say that every man is the center of his own universe, that no two of these personal worlds are alike and one may never hope to experience any but his own. For each man the horizon includes the disk of land on which he stands, and move where he will, he is always at its center. As no man can stand on the spot another stands on at the same time, so no man's universe is ever quite like another's. Each is unique in space and time, and is never quite the same in succeeding moments. As one moves through time and space, so does his universe, and only in a given instant will he find permanence. Change is the universal law: change with never a moment of rest.

Thus bound within himself, how is man to know the "real" universe? If astronomers, physicists, mathematicians, and philosophers are on the right track, the subjective world of the senses is far more tangible than the "real" or objective world. It has even been suggested that the objective world, since it resolves into nothing more than a series of events in space-time, is closely akin to thought itself. Perhaps it may be said that there are many universes, all within each other and superimposed. The objective universe of ultimate reality which exists beyond the senses must contain all these, and may perhaps be thought of as a composite of all the personal subjective universes. We spend most of our time in our own personal universe, but we must not forget that somewhere within and about it lies a strange and unfamiliar framework-universe. It is a confusing and disconcerting picture in which the "real" world becomes a thought and the familiar world of our senses becomes an illusion. Yet that is essentially what happens.

A rainbow will illustrate some of these

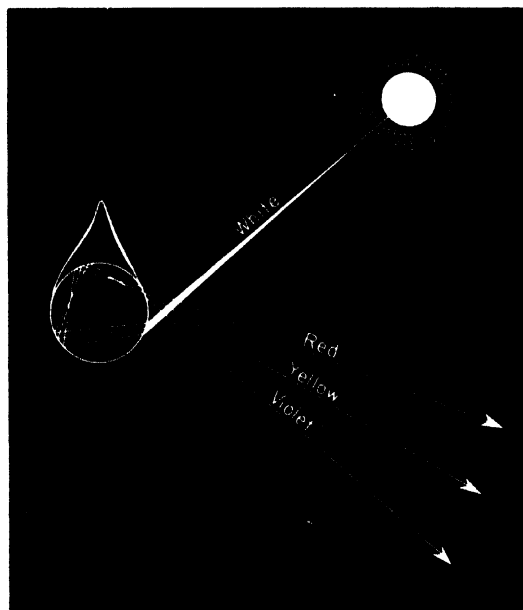


Fig. 1. How a drop of water refracts and splits a beam of white light.

abstractions. What is the rainbow? We can see it, but in what sense is it "real"? One step beyond the rainbow is a cloud of raindrops. Each drop catches the "white" light of the sun and splits the beam of light into a fan-shaped array of colors. Dewdrops do the same thing when they sparkle like diamonds in the grass. Each color represents a special "wave length" of light and is released from within the raindrop at an angle precisely determined by its wave length (Fig. 1). Out of each drop the same color emerges at the same angle with respect to the beam of white light that went in. In order to find the location of all the drops in which the emerging beam that strikes the eye makes the same angle with the beam of white light that goes in, imagine as many lines as possible stretched between the eye and the surface of a wall in front of the observer with each line at an angle of 30 degrees to the wall. The result would be a cone, and all the points on the wall would be arranged in the form of a circle. Similarly, the drops in the sky that send a beam of red light to the eye would be arranged in the form of an arc (Fig. 2). Different bands of color strike the eye from drops

above or below, since these colors emerge at different angles. Furthermore, since each drop is in motion, it will send only an instantaneous flash of a given color from a given position, to be replaced instantly by another drop which repeats the performance. Since the location of the circle of red light is determined by the observer's position, the rainbow *you* see is *your* rainbow, and cannot possibly be the one your neighbor sees. So the static rainbow turns out to be the projection of a series of events between the sun, the raindrops, and the eye.

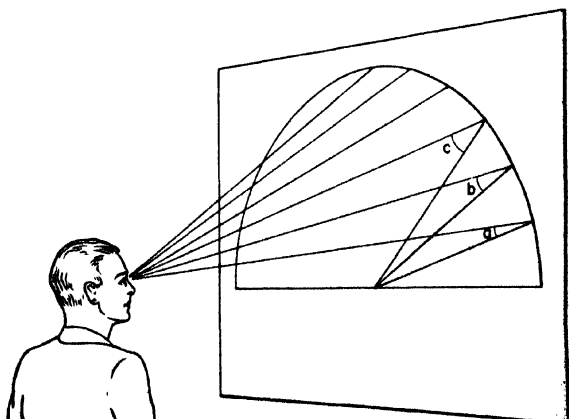
Considering other aspects of the world, one may come to feel that the whole subjective universe is much like that. Yet men will continue to attribute reality to this illusory world. They will still speak of rainbows, though with certain reservations. And it is right that men should speak of rainbows — though they should also understand that rainbows exist in this other way as well.

THE EXTENT OF SPACE

Polaris, the North Star

Since it is our present purpose to find man's place in this objective universe, let us first see how science pictures it today. In the northern heavens sprawls the familiar Dipper. Follow a line upward from the front of its cup about five times as far as these two stars are from each other to a fainter star: Polaris, the

Fig. 2. Lines of sight. Since all light of each color leaving a rain-cloud emerges at the same angle with respect to the observer's eye, each band of color in the rainbow is a segment of a circle. (See text.)



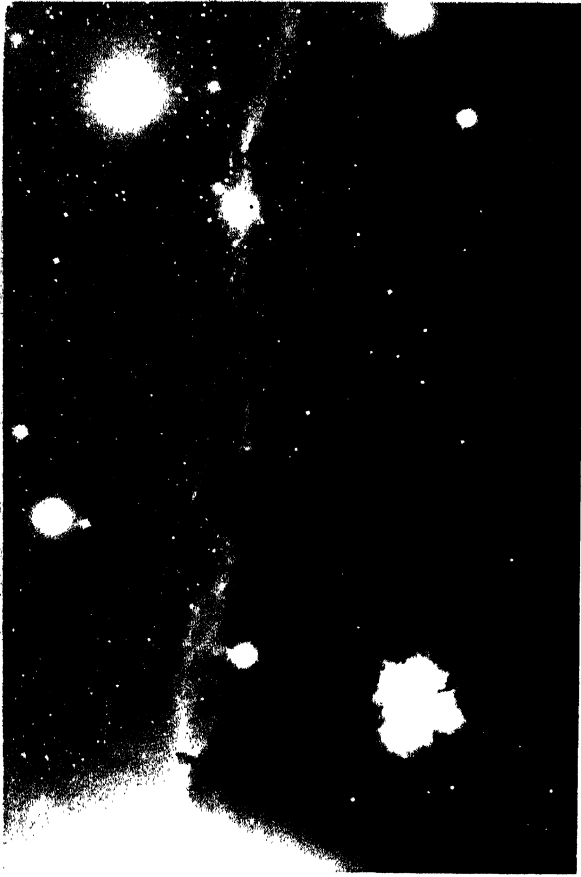


Fig. 3. The "Horse's Head," a dark Nebula in Orion.

North Star. The observer will say "I see it," and he does, as surely as he sees anything. But strictly speaking, what he sees is light that left Polaris about 300 years ago. Three hundred years ago this flaming star sent out a message, part of which has reached a human eye tonight, there perhaps to fan the flame of imagination. This message leaped into space at the prodigious speed of light — 186,000 miles a second — and for three hundred years has been vibrating through the vast reaches of space. Each second of that time it covered more than seven times the distance around the equator of this globe. Some of that light happened to intersect the future path of the earth and thus, three hundred years later, to fall upon the eye.

Think what a span of space and time it covered. Leeuwenhoek was experimenting with his first microscopes and Galileo was constructing the first successful telescope when this

ray of light left Polaris. It was well on its way when Sir Isaac Newton was born, but it was still far from its journey's end when he died. It traveled while three centuries of human events have multiplied man's history. Although this light is little more than a speck to the human eye, it can be dazzling to the mind behind that eye. Does it mean, then, that when one "sees" Polaris he is looking three hundred years into the past, that he sees it where and as it was three hundred years ago? That is as close to the truth as we may hope to come at this point.

Now let the mind reach out across these three hundred light years in an instant. It is not easy to comprehend these distances. Three hundred light years expressed in miles has very little meaning. *One* light year is calculated by finding the number of seconds in one year and multiplying by 186,000. Approach this star within a few million miles and examine it more closely. It need not be amazing if Polaris turns out to be not one star but a system of three or perhaps four stars. Such systems are numerous. But let us approach one of the stars that compose Polaris.

Ahead lies a vast expanse of flaming gas. The physical eye could no more look into it than into the heart of an exploding atom bomb. In fact, this star, like all stars, may be thought of as a chronically exploding atom bomb of immense size. Monstrous flames, thousands of miles long, lick out into the blackness of space. Polaris reveals itself as a system of gigantic, blazing suns. Beyond and all about extends black, empty space, separating it from countless other gleaming stars, each one a distant flaming sun or group of suns.

The Milky Way

But Polaris is only a first step. Leap now from star to star, ever deeper into the glittering galaxy, the Milky Way. With the speed of thought large stars pass, and smaller ones; bright ones and dim ones, some as black as night; single stars, pairs, and intricate systems of spinning couples around spinning couples. We pass suns with darkened spheres revolving

around them and perhaps with planetary systems like our own. We pass immense globular clusters, each composed of hundreds of thousands of stars. We see apparently endless reaches of black clouds and luminous clouds that fade into nothing as we pass into them, so thinly is their substance scattered. But we also pass through showers of cold debris that are very substantial. At the end of this journey we shall have traveled 200,000 light years, and we shall have passed quite through the Milky Way, the galaxy of which earth is a part.

On such a headlong flight through space it is not easy to grasp the significance of the forms of matter seen. The keenest minds have just begun to guess their meaning. Let us re-examine some of them. Astronomers say that the cloud-like galactic nebulae, which melt away as we approach, put to shame man's best attempts to produce a vacuum, or "empty" space. Whereas the lowest vacuum man can produce contains so much matter that each atom is still subjected to 1000 collisions a second, the atoms in a nebula are so far apart that they may not collide more often than once an hour. Yet this cloud is so vast and contains so much matter, in spite of its rarefaction, that perhaps a dozen stars like the sun might be made of it. Intensely hot stars radiate showers of energy into the thinly scattered atoms of some such nebulae, exciting them to luminosity. Others, lacking this exciting influence, are non-luminous (Fig. 3). These are the dark nebulae that resemble huge black thunderheads and blot out the bright stars that lie beyond them.

The globular star clusters form clannish families within the galaxy, each consisting of hundreds of thousands of stars. Thus is composed the Milky Way, of which earth and the sun are members. Inserting the elements of time and distance will give a fair picture. Two hundred thousand light years lie behind: two hundred thousand years, one hundred times the span of the Christian era. That is the time it would take a light signal to travel from one edge of the Milky Way to the other. That, in other words, is its diameter.

The Universe Beyond

At the edge of our galaxy, the stars thin out and we pass them less frequently. Is this perhaps the end? The Milky Way is called an "island universe," but we must not be misled by this inaccurate term. At the edge of our star family, a distance of 200,000 light years from earth, we have not yet left "home." There are immeasurable distances beyond.

At the edge of the galaxy is a vast abyss, the blackest, emptiest space, apparently quite void of matter except for the faintest twinkle in the distance, as of the smallest mote of dust. Far out are scattered fuzzy specks of light. Now if we go again the distance we have come, another 200,000 light years into space and then look back, no superlative will do justice to the view. Stretching vastly across the velvet-black heavens is a glittering whirlpool of stars, all the billions of them in one incredible spiraled disk. One of the minute motes of shining dust within that multitude is the sun. That is our island universe behind us (Fig. 4). Even at a distance of 200,000 light years from the edge of our galaxy, the "fuzzy stars" scattered at the rim of our larger universe will not have grown appreciably in size. Another million light years forward, and one of the faint pin-points of light will have grown until it spreads across the field of vision. Ahead now lies the same grandiose spectacle upon which we turned our backs a moment before, but this time it is not *our* galaxy, which lies over a million light years behind; it is another star family: billions of stars of the same majestic splendor.

Behind now, faintly gleaming in the blackness, star upon star twinkles in seemingly endless array. Each one of these — and there are millions of them — is a mighty "island universe" like the Milky Way. One of these millions, unidentifiable among the multitude, is our own galaxy. Deep within it revolves our sun, an average star among the billions. Around this speck within a speck revolve far tinier motes of burned out cinders — the planets. One of these, of modest size compared with the rest, is Earth.

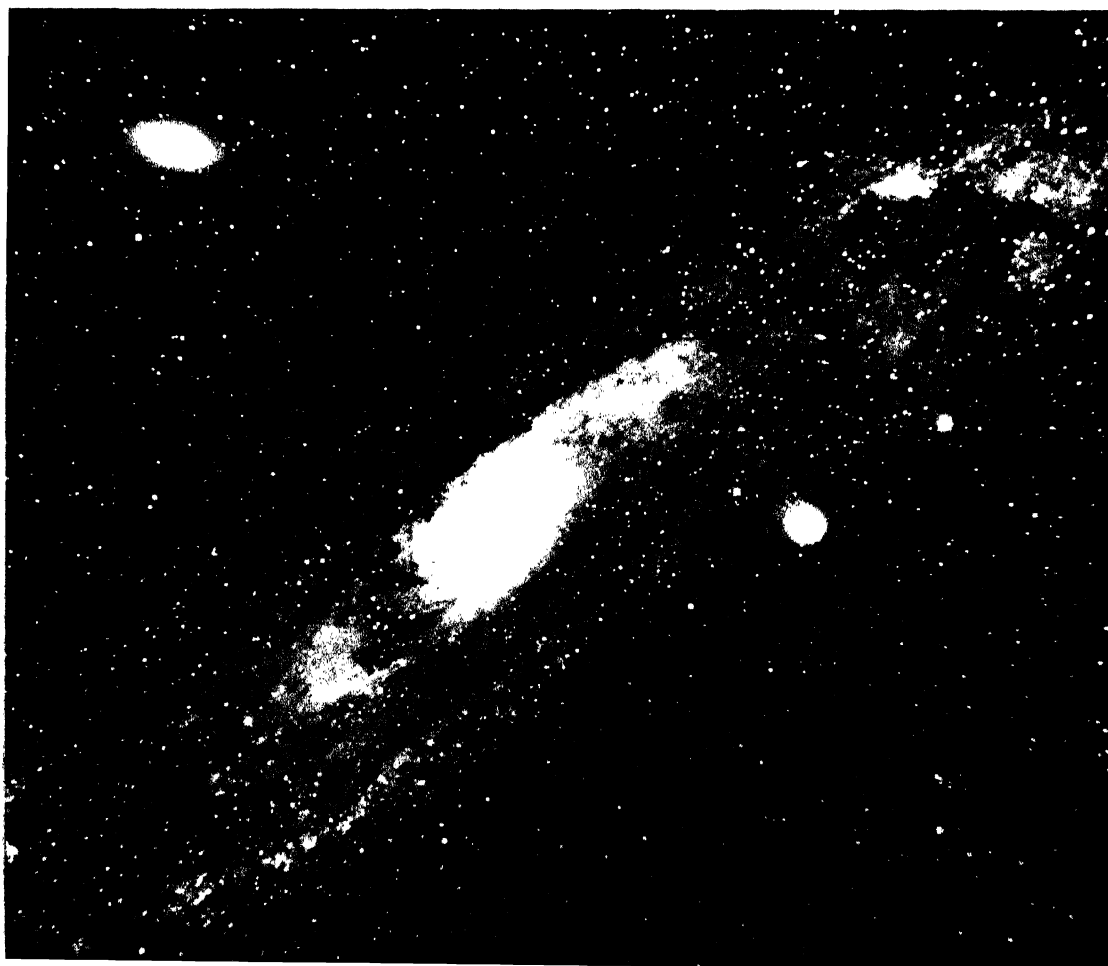
A MODEL OF THE UNIVERSE

The universe is so large that no mind can visualize it, and even the little of it that can be reached with the telescopes is so immense, compared to objects within the size-range of human comprehension, that no adequate scale model can ever be made of it. In a model large enough to show the earth as a barely visible dust speck, the star nearest the sun would have to be placed 250 miles distant. On this unwieldy scale the diameter of our galaxy would be 10 million miles. Clearly, no one scale will suffice. It will be necessary to use successively smaller scales in order really to visualize the size and distance relations of the main structural units of the universe.

Three Scales of Size

On a scale which reduces the earth to a diameter of $\frac{1}{8}$ inch, the finest dot that can be made with a sharp pencil will approximate this size. The sun, with approximately 100 times the diameter of the earth, would then be $\frac{1}{8}$ of an inch in diameter and four feet from the dust-speck earth. Jupiter, the largest of the planets, would be a sand grain $\frac{1}{8}$ of an inch in diameter, about 20 feet from the pea-sized sun. The most distant planet would be the dust-speck Pluto, 160 feet from the sun. The diameter of the solar system, measured across the orbit of Pluto, would be 320 feet. In this model Proxima Centauri, the star nearest the sun, would be 150 *miles* away!

Fig. 4. The Great Andromeda Nebula, an "island universe" similar to our own.



Here stop and visualize:

Earth — a dust speck

Sun — a pea

Diameter of solar system — an assembly hall

Distance to nearest star — 150 miles

Diameter of Milky Way — 6 million miles.

How empty this galaxy is with all its 100 billion stars, more or less! A pea here — that is the sun; another pea 150 miles away, a neighboring star. Another star 150 miles from that, and so on in all directions. How far? *At this scale*, far enough to form a flattened disk-like swarm 6 million miles across. In all this thinly scattered swarm, the sun is insignificant, the earth a mote of microscopic dust.

In order to bring the universe within comprehensible limits at the larger end, it is necessary to reduce it below the limit at the smaller end. So if we reduce the sun to a speck $\frac{1}{8}$ of an inch in diameter (the size we made the earth in our first model), earth now becomes an invisible microscopic particle $\frac{1}{2}$ inch from the sun. The entire solar system with all its planets is the size of a wagon wheel 3 feet in diameter. One and a half miles away from the sun is another dust-speck star, Proxima Centauri. Here in this crowded community of stars, our model shows a dust speck here, another a mile or two away, and so in all directions. These dust specks form a flattened cloud or swarm, which measured on our new scale is 60,000 miles in diameter. Thus on the smallest scale that will show individual units as visible specks, a model of our galaxy would stretch almost a quarter of the distance from the earth to the moon.

Clearly, to grasp the larger picture, the scale must be reduced again. The sun and the planets will be *sub-microscopic*, and the *entire solar system* a dot of $\frac{1}{8}$ inch. Now Proxima Centauri, which would be microscopic, would be only 15 inches away, and the *entire galaxy* would stretch over an area of "only" eight miles. Millions of such 8-mile disks would be scattered 50 to 100 miles apart in all directions. From the invisible sub-

microscopic earth, man's most powerful telescopes reach out and detect light signals from galaxies 5000 of our "miles" away. And this is not the end of space; only of the space that man has probed.

Motion and Speed

So far our model has been a still picture of an animated scene. To complete it motion must be added. The earth spins about its axis, as do all the planets; these follow their paths around the sun; the sun, with all its planets, weaves its way between its neighbor stars; the entire galaxy revolves majestically like a giant wheel. Finally, the galaxies move about in space with reference to each other, possibly showing a tendency to scatter in all directions. These are the motions in which man participates all unknowingly.

Now try to visualize the relative speeds (Fig. 5). The highest reasonable speed reached in a car on a good highway will be not much more than 60 miles per hour. Modern high-speed planes reach 600 m.p.h. and more. New jet-planes have broken the "sonic barrier" and may approach speeds of 1000 m.p.h. At the equator, the surface speed of the earth as it revolves around its axis is 1000 m.p.h. Rockets may attain a speed of 3000 m.p.h., but the sun weaves its way through the stars at the rate of 45,000 m.p.h., while the earth courses around the sun at the still higher speed of 66,000 m.p.h. The speed of the galaxies with reference to each other is quite fantastic — over 600,000 m.p.h. Yet, compared to the speed of light, all these are slow, for light travels at nearly 670,000,000 m.p.h.

Let us reduce these speeds, as we have reduced the sizes of the heavenly bodies, in order to fit them into our model. We can do this easily by calculating the speed in terms of the object rather than in miles per hour. Since the sun's diameter is 864,000 miles and it moves at 45,000 m.p.h., it travels the distance of its own diameter in about 20 hours. The enormous size of the sun as measured by terrestrial standards becomes evident from this. If the sun were suddenly to head for the earth at its

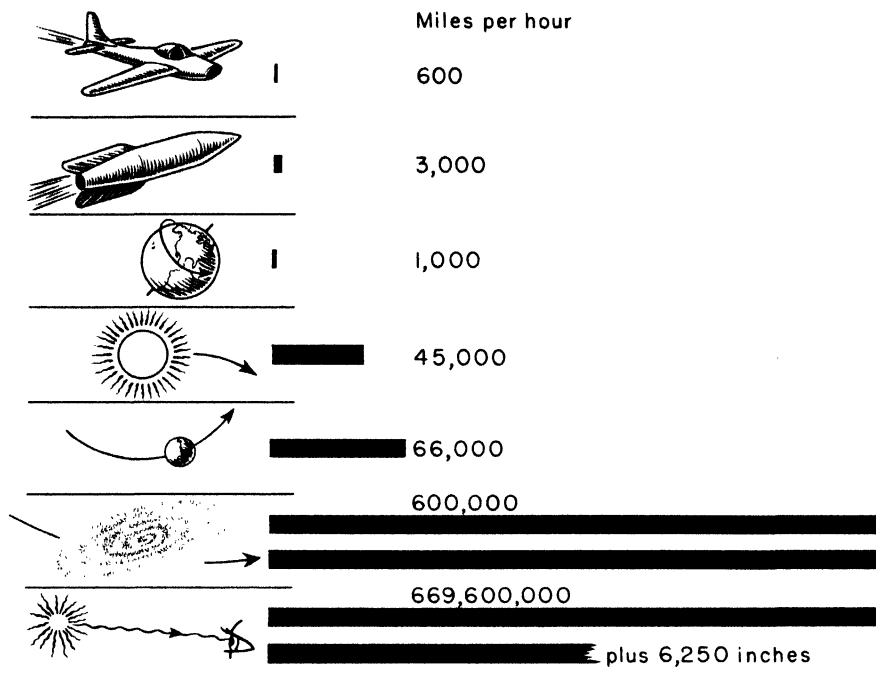


Fig. 5. A scale of speeds.

normal speed, and if the earth were to remain stationary in space, the sun would require over 2000 hours, about 83 days, to reach the earth. Applied to our last scale model of the universe, this means that despite its enormous speed in miles per hour, the sun would traverse the diameter of the solar system, $2\frac{1}{50}$ inch, only after 20 years. Within the normal human life span, that is, it would travel less than the diameter of the period at the end of this sentence. During this same lifetime, the entire galactic cloud with its ten mile diameter would have moved less than $\frac{1}{5}$ of an inch, and light from the galaxy would have streamed out only seventeen inches.

The universe has been referred to as "an animated scene," and so it is, for surely 600,000 m.p.h. is hardly standing still. Yet if one stood back and viewed this animated scale model, it would appear stationary. Despite their terrific speeds, the stars remain "fixed" in that perspective which their distance gives them.

In such a universe there is no up or down, no standard time, no fixed point anywhere by which to judge absolute direction or rate of

movement. We can only refer to position or movement with reference to some other unfixed object. There is no static marker of any kind. All is motion — be it relatively ever so slight — and change. Despite the vast numbers of gigantic stars, their numbers and their size are dwarfed by the immensity of space. And if the stars are dwarfed, what then of earth, which might be packed inside the sun a million times over? This is the stage on which life has evolved, so immense a stage that it all but crushes life into insignificance.

THE RELATIVITY OF TIME

Consider now that other strange "dimension," time. A point in space can be fixed relative to the earth by its longitude, latitude, and altitude. But since earth is far from stationary, a point determined relative to it is certainly not absolutely determined in space. And since there is no fixed point in space to which an object may be referred, its absolute position can be determined only at a given instant — and there the dimension of time becomes a factor. This is as far as we can pene-

trate these problems here, but we can try to understand how subjective our sense of the "speed of time" must be, and how intimately it is tied up with the length of our life span and our rate of living. Let us illustrate.

We may begin with a scene as it appears to us, a pond surrounded by pines. It is night, and the stars accentuate the vast extent of space. With their enormous speeds nullified by distance, they look like motionless brilliant pin-points in the familiar constellations. Fireflies weave against the pines and the sky, and all these patterns, still or moving, are reflected in the pond. A frog is croaking and mosquitoes whine. The earth is solid under foot, and the world seems stable and peaceful.

These are the things we perceive with our senses. But how much of this is an extension of our minds? The interpretation of time, as of space, depends upon the viewpoint. In the tempo of everyday life, a thousand years seems long indeed. But to someone steeped in the study of paleontology, thirty thousand years may seem but an instant, and a variation of this amount in a geologic era, inconsequential. It appears quite certain, though, that the length of the human life span largely determines whether we consider something *slow* or *fast*.

To see how this may be, let us invent imaginary creatures with exaggeratedly brief and long life spans and call them Minim and Chronos, respectively. Minim's life span shall be as fleeting as the fraction of a thought. While we ponderously wink an eye, four or five of his generations pass. If he stood by the pond, here is now he might describe what he saw:

"The universe is an immense black expanse of space, studded with myriad specks of light. Some of these specks are nestled among the spear-like, inert matter called grass. Others are suspended in the air all about me, held there by an invisible force, while still others appear to be suspended far out in space, no doubt held there by the same mysterious force. Huge dark masses of inert and apparently everlasting matter, called trees, surrounded me.

A peculiarly formed, inert, and motionless lump of matter called man forms a mound beneath the trees. No sign of motion or life has ever been detected in any of these objects. All of them are as unchanging and unresponsive as the things called stones which also lie all about. In fact, the world is motionless, unchanging. We, the Minims, appear to be the only creatures endowed with life and motion."

Thus Minim might describe his universe, and what a different universe he sees! His world is black because his life span happens to come at night. To him the fireflies are as motionless as the stars, because in the $\frac{1}{100}$ part of a second that he lives, the streaking fireflies do not move enough for their motion to be perceived. Wind, the quivering of a leaf or of a blade of grass, do not exist for Minim. No sound within the range of human hearing would be audible to him. Stories of the far-off period when the world was bathed in sunlight would not, even in the form of myth, come down to the nocturnal Minim generations. An hour of our time would be as 25 million years to Minim. There is no more motion in such a world than in a photograph.

Now visualize a time far slower than human time, and a creature as sluggish and long-lived to man as man is to Minim. We shall call this creature of near-eternity Chronos, and just one of his slow-moving hours would in our reckoning be 25 million years. This is how the same pond might look to him:

"Everything in the universe flashes and squirms with disconcerting speed. Most things exist but a moment and flash out of existence. There is no fixed, firm point on which to rest the eye. A moment ago as I sat down (it took him 15,000 of our years to do so), there was one of those ephemeral things called a pond before me. By the time I was seated it had disappeared, as such mirages do. The earth is a thick fluid that undulates in a series of waves or hills. Valleys are dangerous with wicked writhing streams that eat into the land. Most of the surface of this heaving earth is covered with an intangible, turbulent green stuff, which may persist some minutes

and then disappear completely, only to flash back again for an instant the next second. A few minutes ago, the world was covered briefly with a white fluff, but this too faded away.

"Overhead is a great expanse of space, divided into distinct halves. One half is a uniform gray: the other is bright and shining. In the gray area I dimly see a squirming pattern of nearly concentric spirals or circles. The shining half of the sky is bright and unchanging, and a warm light comes from it. On the earth I see no moving object, no organized creature with a life such as mine."

This is the world of Chronos, to whom 7000 years are but a second. How could his world be the same as man's or Minim's? Actually, all three worlds have the same setting in *space* but are differently set in *time*. Hence the three subjective impressions are totally different.

To us a pond is as enduring as the light of the firefly is to Minim, but for Chronos it would probably have vanished as soon as he glimpsed it. The average tree germinates, matures, decays, and dies in less than $\frac{1}{30}$ of one of his seconds. He would not see even the long-lived Sequoia; only the green haze which alternately spreads and disappears.

To Chronos the slow process of erosion, the grinding away of mountains by wind and water, frost and heat, would be a visible flowing and sliding. Night, day, and the seasons would not exist for him. In one of his seconds the sun rises and sets two million times. He would have lived through the last ice age in a moment, but it would not have lasted long enough to produce a sensible chill in his frame. He would not see the sun, but an arched band of light; or the stars, but weaving spirals.

Finally, to Chronos all the life that populates the earth is less than fleeting shadows, invisible and beyond the range of his senses.

THE OBJECTIVE OR "REAL" WORLD

The worlds of Minim, man, and Chronos are all subjective interpretations of the single "real" world that lies beneath them. Surely

one must wonder, seeing the worlds of Minim and Chronos, how far the human subjective world deviates from the objective one.

Slowly man is learning to reason less subjectively. No longer is he shocked to know that neither his earth, his solar system, nor even his galaxy is the center of the universe. Such habits of thought, however, die slowly. Even today some astronomers have felt impelled to proclaim that in a sea of island universes, our own galaxy would have the distinction of being a continent. Most scientists might concede such a possibility, but they would view it with suspicion, for, if true, it is probably no more than a mere coincidence. Today we humbly, yet with no little satisfaction, bow to the realization that our own galaxy is probably no different from all the rest.

Gravity: Binder of the Universe

Merely to accept the facts you observe does not constitute scientific understanding. Facts must be interrelated and that requires vision and contemplation. Imagine a stretch of beach across a cove. It is just past ebb tide, and here and there a tide-pool has remained in its rocky basin, precariously sheltering multitudes of creatures awaiting the return of the sea.

Time passes, and almost imperceptibly each wave rises a bit higher than the one before. There is no violence, no obvious display of power, and yet the great Atlantic steadily rises, lifting the tremendous masses of water and all the ships they bear. What an enormous force this represents; what power there must be behind this fact. The force at work is gravity.

Newton's Concept of Gravity. It was Isaac Newton who in a moment of insight first observed the universality of this force. Every school child learns that Newton was apparently the first man to watch an apple fall. That, of course, was no new observation. Nor was it news that objects fall towards the earth. What Newton really achieved was the prodigious feat of grasping the universality of this phenomenon — the feat of guessing that the

force which caused the apple to fall was the same force that holds the moon in its path and makes the oceans rise and ebb. He expressed this by saying that between any two particles — such as the apple and the earth — there exists a force proportional to their masses and inversely proportional to the square of the distance that separates them. This means that an object with twice the mass will be attracted with twice the force; an object twice as far away will be attracted *inversely* with the *square* of its distance, or $(\frac{1}{2})^2$, which would be $\frac{1}{4}$ as much. An object three times as far away would be attracted $(\frac{1}{3})^2$, or $\frac{1}{9}$ as much, and so on.

These are statements that can be experimentally checked and verified, for they are merely expressions of fact. They do not, however, explain what gravity really is. They merely state that it is a force, and how this force behaves. Modern astronomers, physicists, and mathematicians have evolved new concepts of time and space which at first appear very strange to our earthbound minds, concepts which have made it possible to predict and to account for phenomena that previously were baffling. These scientists dismiss the concept of absolute position and absolute time, and since these conditions are involved in Newton's interpretation of gravity, they dismiss his concept of gravity, too. It is impossible here to give a satisfactory explanation of the modern concept of gravity, for that could be done only in the language of the mathematician. However, gravity, whether thought of in the concepts of Newton or of Einstein, is an aspect of nature to which living things are adapted and by which they are conditioned.

We shall continue to speak of gravity as an attraction between objects, just as we continue to speak of a rainbow, and the "rising" or the "setting" of the sun, although we know that the rainbow seen is different from the objective one and the sun does not rise or set. Whatever the nature of gravity, it appears that we must look upon it as the "binder" that holds the universe together. Hence we shall speak of the "force of gravity" for the sake of clarify-

ing a picture otherwise almost incomprehensible. In some manner this force, and perhaps variants of it, results in the balance and stability of the universe. The earth and all its particles hold together because of it. So do the sun, the planets, and all the stars and galaxies. By invoking it we come one step closer to understanding such phenomena as the tides, the movement of the planets, and indeed their very creation. In fact, the genesis of the entire universe in its present form may tentatively be explained as a result of this force.

COSMOGONY

The Changing Universe

The question of ultimate origins is naturally insistent at an early stage in any exploration of the universe. No inquiring mind can escape it, even though there may be little hope for a specific and ultimate answer. The question resolves itself to this: How did the universe begin? Where did it come from? Why did it shape itself as it is? And finally, perhaps, why is the universe? That last one, of course, is the ultimate question, and that it should ever be answered appears unlikely. But not all these questions are unanswerable.

It appears obvious today that the universe could not always have been as it is now, though that was not so obvious to our ancestors. Today we perceive its dynamic nature. Everything is in motion, everything appears to be changing from one form to another, from one state of being to another. The universe does not have the fixed unmoving quality of a tapestry, but moves like a display of fireworks against a night sky. A snapshot of such a display would show a clear, sharp pattern; but if this were compared to a snapshot taken before or after, the pattern would be changed. The very law of the universe appears to be change. So it seems obvious that the universe must have been different in the past, that once there must have been no pattern, and that somehow and somewhere in time the evolution of a pattern must have had a beginning.

Speculations on the origin of the universe are probably as old as man. Primitive mythologies are full of naïve accounts of giants and gods creating worlds and stars, but such accounts are no longer satisfying, for they are not based upon observable facts. Although it appears that man must never expect a final answer, since each answer inevitably carries in it the seed of a new question, yet he still seeks and finds satisfaction in each partial answer. Today men are impelled to explain all matters in a "natural" way and inclined to consider the word "supernatural" as synonymous with "ignorant." The "science" of the savage who explains the airplane by saying that it is endowed with the spirit of flight is not acceptable. But we must be on guard against a similar error, that by naming a phenomenon we believe we have explained it. Names are useful labels, but they are not explanations.

Cosmic Evolution

The problem of the origin and formation of the universe and all that is within it is a profound one. Recall our voyage into the farthest reaches of space and time, where we saw that distant stars are flaming suns, scattered through space in unimaginable numbers, galaxy beyond galaxy. None of these, if the concept of the law of change is true, are permanent or finished structures. Rather, these spiral nebulae are majestically evolving star-systems, slowly running their perhaps predestined course of evolution from infinitely tenuous masses of gas to star groups composed of countless millions of single stars or star systems, and some, quite possibly, with planetary systems similar to our own. This is the picture as we see it today; it may be modified in the future.

The constructing of this picture goes back to Newton, who first approached this problem on a scientific basis. Although his theories were largely speculations, it is remarkable how many of his speculations are still current, perhaps in modern dress. Newton, like Kant and Laplace after him, pictured a limitless expanse of unorganized primordial matter as the raw

material from which the universe was shaped. Modern scientific leaders still picture a limitless, if finite, expanse of evenly distributed matter as a starting point, though today it appears that we cannot talk about "the" starting point.

Origin of the Universe: Modern Hypothesis

The modern hypothesis can be phrased as follows: In the beginning was a limitless but finite curved universe, determined in size by the amount of matter in it, all of which was evenly distributed in the form of a thin gas. Assuming that matter is distributed throughout space in approximately the same amount as it is in those parts of it which can be surveyed, the total amount of matter in the universe can be estimated, since the size of the universe appears to be determined by the amount of matter in it. Dr. Edwin Hubble of the Mount Wilson Observatory has estimated the density of matter in a universe so constructed. Under these conditions it appears that only a single molecule could be allotted to every 1000 cubic yards of space. This represents a degree of "emptiness" never attained on earth, even in the most perfect vacuum achieved in scientific laboratories. Matter thus uniformly and evenly distributed would tend to remain undisturbed by gravity, since this "force" would be equal in all directions. But any sufficient disturbance that would crowd a mass of molecules together at some point could upset the equilibrium of the entire system. It would create a landslide effect, for the molecules so crowded would exert a mass gravitational pull on the less crowded molecules around them. Such a disturbance, or wave of compression, would have to be of sufficient magnitude, for otherwise the compressed molecules would simply scatter again in all directions.

Sir James Jeans analyzed the problem of gravitational instability mathematically and obtained a formula by which it was possible to determine the average distance between such condensations of matter previously distributed uniformly. This led to a striking coincidence:

the distances so computed were found to correspond almost exactly with the mean distances between the great spiral nebulae.

From this point on, the evolution of these spherical masses of gas is more clearly understood. Yet we must make one more assumption, namely that the original ocean of primordial matter was not completely at rest, but that there were currents, eddies, and drifts in this thin sea of gas. The nature and origin of these currents is another unanswered question, but whatever it was, they would remain even after the "curdling" action of matter had begun. In fact, such movement would not only be maintained; it would become very much accentuated. If the diameter of the orbit of a body rotating about a center is shortened, its rate of rotation increases with the shortening of its orbit. Such rotation set up in a shrinking sphere would tend to flatten it, so that it would finally become disk-shaped, and parts of it flung off at its equator would produce spiral arms. In this description we recognize the spiral nebulae.)

Cold reason unsupported by imagination cannot grasp the immensity of this creation. One may be tempted toward mysticism in the struggle to visualize the inconceivable magnitude and the fatefulness of these events. Slowly these great clouds gyrate and spiral. Irresistibly the collective gravitational force of these countless particles causes them to fall toward the center of the newly formed mass. For millions of years they draw together, becoming more agitated as they do so. The almost imperceptible rotation becomes more and more pronounced, until as the nebula spins faster, a new force begins to assert itself. Centrifugal force begins to distort the original sphere. Slowly the great gaseous ball becomes flattened, and its axis continues to shorten until at last the whole mass assumes the shape of a great double-convex lens. As this occurs a straining and tugging commences at its outer edge as the conflict between gravity and centrifugal force becomes more acute. Ragged fragments tear themselves away to form dazzling spiral arms, strikingly similar to those of a

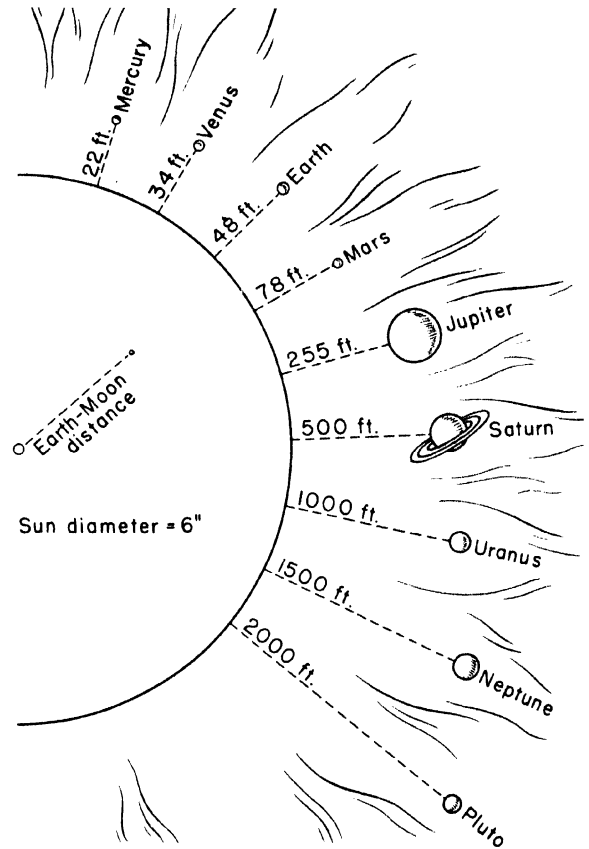


Fig. 6. A scale model of the sun and the planets.

fiery pinwheel. The same force that formed the mother-mass now causes these wisps of matter to condense into spherical particles. As a thin stream of water trickling from a faucet breaks into individual drops, so this nebular mass breaks into gigantic beads — and stars are created. As this process continues, more and more stars are born, and gradually the structure of the galaxy changes with its age. Telescopes reveal more than two million island universes like our own galaxy, some younger, some older, their age revealed by their structure. Many times two million more must lie beyond the range of telescopic vision.

This is a thumb-nail sketch of what astronomers now think happened. Much has been left untold and may merely be hinted at here. What of the stars? Since some are old and some are young, the history of their evolution may be reconstructed by arranging the visible

specimens in suitable evolutionary order. We are still largely ignorant of the sequences of their changes, but it is fairly certain that stars are born, pass through a fiery youth, age, and probably die, that is, become cold, inert masses. There may be rejuvenations and perhaps reincarnations. Future studies will probably clarify this hazy picture. The terrific internal pressure created by the condensation of matter releases continuous and inconceivably large amounts of intra-atomic energy. Indeed, the stars may be likened to chronically exploding atom-bombs. This is the source of their brilliance and of the sun's. Should the thought occur that perhaps all this was determined from the beginning — that all this had to happen just so that life might follow — do not discard the idea as utterly preposterous. The person who thinks so will find himself in good company. The idea of causality and strict determinacy has been vigorously attacked in these past years, but there are also men that loom large in the sciences who are not convinced. Einstein is quoted as saying, "Indeterminism is quite an illogical concept. . . . Now I believe that events in nature are controlled by a much stricter and more closely binding law than we suspect today. . . . Quantum physics has presented us with very complex processes and to meet them we must further enlarge and refine our concept of causality."

CREATION OF THE SOLAR SYSTEM

The fate of one star, the sun, must receive our special attention, not only because it provides heat and light and thus makes life possible, but because earth and the planets may be its actual physical offspring. Numerous theories have been advanced to explain the creation of the solar system, but none accounts for all its peculiarities. It has been thought that the forces that produced the spiral arms of the great nebulae might also have produced the planets. It appeared quite reasonable that the sun, as it shrank in upon itself, spun so fast that fragments of its surface were torn out at its equator by centrifugal force and thus

formed planets. It is known that the sun rotates, for the cores of solar protuberances — sun spots — can be seen to march across its face. The sun is thought to be a gaseous mass. These facts appear to make the above hypothesis tenable, but astronomers say that stars, although we think of them as gaseous systems, behave more like liquids. Indeed, under the conditions existing on the sun, the terms liquid, solid, and gas lose much of their terrestrial meaning. The liquid behavior of the gaseous sun is probably due to the terrific pressure and agitation in its interior. When liquid spheres rotate, they do not tend to scatter smaller fragments around their perimeter as galaxies do. A rotating liquid sphere will tend to break into two fragments of similar size. Such a process would produce double stars — and that is probably the origin of such doublets, many of which exist — but it does not explain the origin of planets. What, then, was responsible for the creation of this solar brood?

The Tidal Theory

One theory is that the sun was once a lone star whose nearest neighbor was probably 25 or 30 quadrillion miles (4 or 5 light years) away, but that another star passed very near it. If this star had been the sun's closest neighbor and had traveled at the average speed of stars, it would have required no less than 500 years for the journey. Visualize this (Fig. 7).

As the two stars come closer, great mountains of heaving matter are ripped bodily from both in massive explosions. Imagine their immensity, since the erupted matter from the sun must equal the combined mass of all the planets and planetoids. Visualize them as ragged trails of flaming sun-matter, shaped into spiral form by the rotating moment imparted by the passing of star past star. The ends of the trail are thinnest, since they were produced when the pull of the passing star was weakest, as it approached and as it receded. The result is a trail of matter shaped like a tapered cigar.

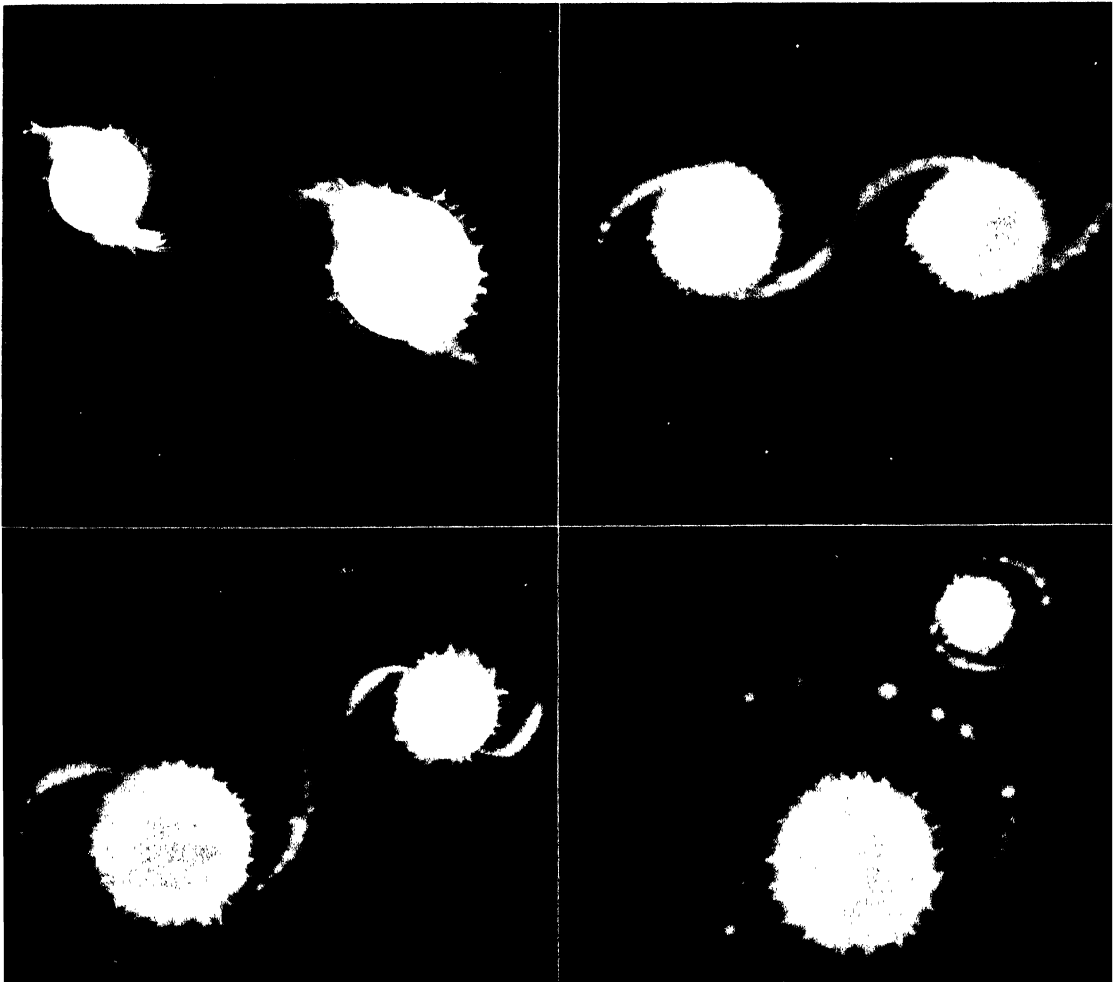
As the activating star rushes away into space, the trail of erupted matter once more

responds to the gravitational force of our sun alone. Hence it falls back, but not along the path it came. Because of its new rotary motion, it falls back toward the sun at a tangent. Since it gathers speed as it goes, it does not rejoin the sun but rushes past it. But the sun retards its flight and finally checks it. For a brief moment the distance of this train of matter from the sun remains fixed, although its tangential movement continues. Then it falls back again, and but for its tangential motion, once more would plunge into the sun. But since its speed increases, its centrifugal force increases, and it once more shoots past the sun from which it came. Thus the elliptical path of the fragments round the sun is

established and continues unchecked unless the energy of the orbital motion becomes diverted into other channels.

This ragged, spindle-shaped train of revolving matter is not yet a planetary system. The fragments vary in size, and the larger ones now act as gravitational nuclei on the smaller particles surrounding them. These larger particles are the beginnings of the planets. As they swing round the sun they coalesce, first into liquid, white-hot spheres which cool with relative rapidity because of their smaller size. Bit by bit the smaller particles fall into the gravitational sphere of these planetary nuclei, adding to their bulk and mass and still further increasing their gravitational power. In this

Fig. 7. The theory of the creation of the solar system by the tidal action of a passing star on the sun.



manner thousands of miles may have been added to the diameters of the original planetary nuclei. Only now has the birth and growth of the planets been truly achieved.

The Collision Theory

This picture of the possible origin of the solar system, presented to us by Moulton, Chamberlin, and Jeans, is but one explanation out of several current today. It is a good picture and explains much, but it appears to have its defects. H. N. Russell and Lyttleton have offered a modification that appears to overcome some of the difficulties, but which still further reduces the probable number of such systems in the universe. Instead of visualizing our original sun as a single star, they think of it as a double star. In their theory, too, a visiting star initiates the creation of the planets, but instead of side-swiping the sun, it is pictured as sailing head-on into the twin star and practically annihilating it, so that its whole nucleus would have been swept away with the visiting star, leaving only smaller fragments scattered about the sun. According to this theory, these fragments were given sufficient angular momentum (spin) to account for the present motion of the planets, while their separate formation proceeded as described above. It is uncertain which story is closer to the truth. The two are so similar in their basic principle that their differences need not be disturbing. (See also Fig. 8.)

ADOLESCENCE OF EARTH

The small, flaming earth-nucleus cooled as it grew, spinning around the sun with its sister planets. The sun continued its slow atomic disintegration, and its warm rays fell upon this mote of earth much as they do today. But there were no green leaves to absorb its energy and no mortals to bask in its light. Its rays struck only the still-hot crust of a planet fresh from the forge of creation.

What change transformed this desolation of hot rock into our verdant earth of rivers, mountains, and oceans? It was a slow process

of easing atomic activity, of cooling accompanied by physical and chemical reorganization, of acquiring a gaseous envelope of atmosphere as the gravitational mass of the earth increased. Many millions of years were consumed in these processes; how many, no one knows.

Through Chronos eyes we may visualize what happened. The fiery earth nucleus flames less fiercely, and as it gathers the fragments in its path, it slowly grows. Perhaps because it is so much smaller than the sun, its rate of atomic disintegration is reduced, whereas this disintegration still feeds the fires of the sun though the earth has long since cooled. The white heat of the growing earth changes to orange, to dull red. Finally the planet ceases to be a visibly radiant body altogether, and it is swathed in the dense mantle of its newly acquired atmosphere.

In time earth cools enough for a thin crust to form, beneath which lies a bottomless sea of molten rock. Water cannot exist in liquid state upon this heated surface, but only as a part of the atmosphere. Try to picture all the water in the seven seas suspended above the earth. Down near the crust of rock the steam would be intensely hot — not the familiar white opaque steam of the tea kettle, but the superheated steam of the modern steam-turbine, as clear and transparent as winter air, but a withering blast to anything resembling life. In the upper reaches of this atmosphere are cooler regions where the superheated steam condenses to form the minute droplets of ordinary steam or fog. Here probably would be a layer of cloud, far denser than any on earth today, rolling black masses of light-absorbing vapor, too dense for even the faintest ray of light to pierce.

In the clearer atmosphere within this envelope of darkness, ceaseless volcanic outbursts vie with flashes of lightning to turn the night into infernal day. As the earth cools and shrinks, the thin crust shrivels, wrinkles, and trembles, for earthquakes never cease. Where the surface cracks, the pent-up pressure beneath spews forth masses of molten

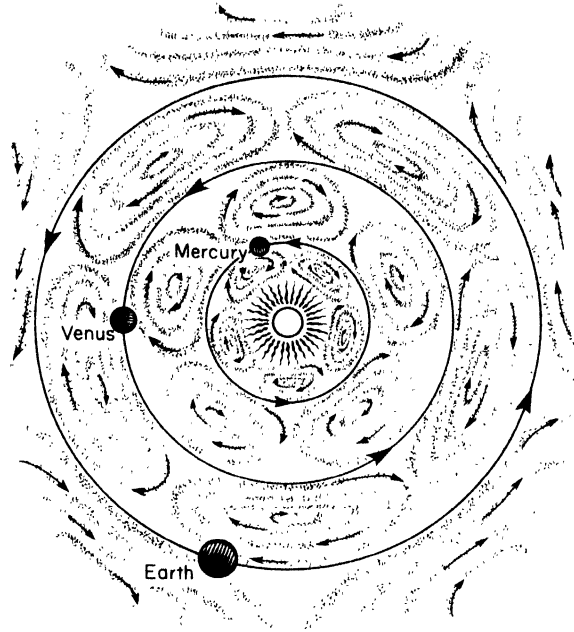


Fig. 8. Another recent theory of the creation of the solar system, proposed by Weizsäcker, is that the planets were formed along the lines of contact between eddies of "dust" moving around the sun.

rock. Then come torrents of rain. At first these are vaporized while falling through the superheated steam near the surface. Then one day the first drops of liquid water strike the earth, hissing upon the rock like drops on a hot stove, then fleeing back into the atmosphere as steam. Another day the downpour strikes the cooling rocks and for the first time stays where it falls. Rivers of boiling water rush down the rocks and form steaming pools and lakes. No longer is the crust sufficiently hot to drive the water back into the atmosphere at once. Water collects, and as it evaporates, more rushes down the new-born stream beds to replace it. The ponds thus formed are the modest beginnings of the world's oceans. This is an event of tremendous importance to all of us, for the oceans are probably the cradle of life.

Formation of Streams and Oceans

As the young earth continues to radiate its store of heat faster than it can be replaced, the

planet shrinks and shrivels further, much like a drying apple. The thin crust throws itself into enormous folds (though slight in relation to the size of the planet) and the earth trembles. Mountains and valleys form. Water cascades down the mountains, seeps through the crevices and fissures of the rock, and settles in the low spots, carrying parts of the crust with it. Thus begins erosion, the ceaseless leveling of what other processes have heaved up. Boulders, stones, pebbles, and sand roll down the stream beds, cutting them deeper into the rock. Low spots are gradually filled. New levels of finer material cover the solid rock. As the grade of a stream lessens, the visible particles settle out and leave only "clear" water. But even this, on its journey over the porous crust of the earth, has picked up much soluble matter, and salts of many kinds are dissolved in it. Carrying this burden, it settles in the low spots and forms the oceans.

The water of a mountain stream tastes sweet while that of the ocean is bitter and salty

because in the former the solution of salts is very weak and in the latter it is concentrated. Not many water particles have time to evaporate during the journey to the sea. But once there, they have all the time in the world, and aided by the warming sun, water particles return to the air as water vapor. The far heavier mineral particles must remain behind. Ages pass, while the mountains are ground down to sea-level by leaching water, storm, and grinding sand. Changes of heat and cold help in this process. Unceasingly, rivers carry their freight of mineral and salt to the oceans. The water evaporates, to be used over and over in an unending cycle, but the salt remains, and the salty oceans thus come into existence.

But the earth is not yet stable or complete. New masses are swept from space and added to it in the form of meteorites. The pressure of this new burden, and further cooling, cause more shrinkage. New mountains form where old ones wore away. Ocean bottoms and their sediment are lifted thousands of feet above their former level, and are worn down once again. Crushed under the weight of accumulated deposits above them, sand, silt, and pebbles are welded into solid rock, preserving within their strata the story of the events that formed them.

The Created Earth

The stable, rock-ribbed earth has taken form. Precariously balanced between its own tremendous momentum and the force of gravity between it and the sun, it steadily pursues its course. Its oceans glisten in the sunlight, while soft banks of cloud sail over it. Rugged mountains cast long shadows where day fades into night. No soil as yet relieves the rocky hardness of the landscape. Only boulders, gravel, and sand cover the surface of this earth.

There is no evidence of life, yet unseen events are taking place which no one yet begins to understand in their entirety. Unknown forces are carrying on the evolution that began with the creation of the universe, shaping and organizing this sun-matter until some day it will become living substance.

The path which we shall follow in subsequent pages is the epic of organic evolution, which began in the primordial space-ocean of thinnest gas, passed through evolving spiral nebulae to vast families of stars, and saw a planet shaped toward the great event of human life. It is to sketch the early phases of this evolution that we have ventured briefly into astronomy and geology as an introduction to the science of life.

The Behavior and Structure of Matter

Life is a part of the world in which it moves, and the stuff of life is the common matter of the universe. Therefore the laws which govern the behavior of matter also govern and determine the activities of living things. But many natural laws produce such familiar patterns of behavior in the world about us that we become all but oblivious to them — if, indeed, we were ever really aware of them at all. We may “know” gravity very well, in the sense that we wouldn’t think of walking out a third story window as we would walk out our front door. But of related matters, we may be quite unaware. Why, for instance, does a rock the size of a fist plummet to the earth when it is dropped, while a particle of dust, which may be composed of the same substance as the rock, will float aimlessly with every gust of air? Or why does a bucket of water, tossed out in the grass, separate into a shower of sprays and drops, while the drops themselves will stick together? Why is it easier to push a car along a level street than to get it started — or to stop it once it is moving?

For most of us, these things, and countless others, “just happen.” But if matter suddenly failed to behave in certain predictable ways — if rain, for instance, were to “fall” upward — we would certainly notice the change, and the chances are that our first reaction would be fright. The savage might explain such erratic behavior in terms of supernatural forces. The scientist would attempt to explain it in terms of known factors, such as hot air rising and producing convection currents; and he would attempt to verify or disprove his assumption. Certainly he would be curious, as we would. But he is also curious about the more ordinary behavior of matter,

and he is constantly attempting to explain it. In a sense, he has much the naiveté of a child about everyday matters as well as unusual ones. To gain some insight into the laws that govern the ordinary behavior of matter and of life, we shall do well to recapture some of that naivete.

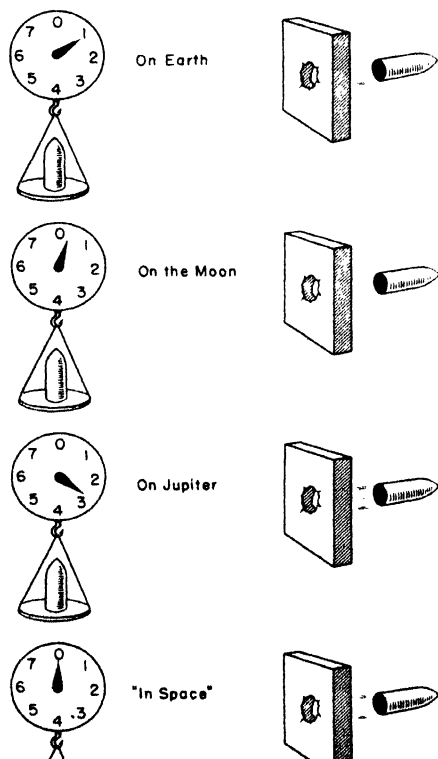
Mass, Weight, and Gravity

One of the basic facts about matter is that it has *mass*, which may be defined as the measure or expression of the quantity of matter in a body as indicated by the amount of *force* necessary to produce a given amount of *motion* in the body at a given time. Newton defined it as “the quantity of matter in a body as measured by the product of its density and bulk.” The concept takes on more meaning when it is remembered that bodies attract each other, as the sun attracts the earth toward it and the earth holds the creatures and objects on its surface. The degree of this attraction is dependent on the masses of the objects concerned, and this in turn gives rise to the phenomenon of *weight*, which is a measure of the forces of attraction between, say, a man’s body and the body of the earth. Thus weight is proportional to mass, and two masses may be compared by weighing them under similar conditions (Fig. 9).

Picture the unseen effect these laws must have on living creatures. An earthly visitor to Jupiter would be crushed to the ground simply by the immensity of his own weight, although his mass would be unchanged. The immense mass of the planet would attract him with such force that his feeble terrestrial muscles could not hold him up. Accordingly, the size of a planet must to a large extent

determine the kind of creatures that could live upon it. Creatures on Jupiter, if there were any, would have to be enormously stocky and strong, hence presumably small and squat. A visitor to the moon from the earth, however, would have only one-sixth his terrestrial weight, for while the moon has but one-eightieth the mass of the earth, it exerts a gravitational pull at its surface one-sixth that of the earth. This is because any object on the moon would be closer to every particle of moon matter than an object on earth is to earth matter, simply because the moon's diameter is smaller and the force of gravity varies inversely as the square of the distance. With his weight reduced to one-sixth, however, a visitor to the moon could do astonishing things. He could easily leap over an average house, or from the top of a hundred foot cliff,

Fig. 9. A bullet propelled by a given amount of explosive will pierce a target with equal force on earth, on the moon, on Jupiter, or in outer space, for its mass and kinetic energy remain the same. But the weight of the bullet depends on the magnitude of the gravitational force acting upon it.



without injury. But collisions would produce the same cuts and bruises as at similar speeds on earth, for his mass would not have diminished. The chances are that a moon-creature could be much less sturdily constructed than one on earth.

Gravity is a powerful force in everyday life on earth, as we would soon see if we could take a rocket trip to a point between the earth and the moon where the pull of the two bodies was canceled out. If at such a point we suddenly stood up in the cabin of our rocket ship, the chances are we would go on floating up toward the ceiling, there to stop with a bump, for there would be no earthly gravity to hold us "down," the mass of the ship would be too slight to attract us perceptibly, and our weight with respect to it would be zero. Moreover, we could not stand, for there would be no force to push our feet against the floor, though we might pull ourselves about by a rope, a handle, or the corner of a seat. Yet if we pushed ourselves over to the opposite wall, we would stop with a thud, for our mass would be the same, even if our weight were not.

Inertia

We would also discover the effect of another force, *inertia*, the resistance of a body to any change in its rate or direction of motion, the tendency it displays to continue at a uniform rate in a given direction. This is the force which, in the absence of gravity, would continue our motion to the ceiling when we started to stand up. But we would also have discovered it, and in a much more painful way, earlier in our trip. In a mild form, most of us have felt this force during the first few seconds of a trip in a high-speed elevator. Pilots pulling out of a power dive experience it more violently in what is called "blacking out." As the rocket leaped into space, we would feel it still more intensely. Savage forces would displace our internal organs, vision would blur, and senses would threaten to fail. The body would be crushed back against the seat as if by a mighty, invisible hand. When the rocket

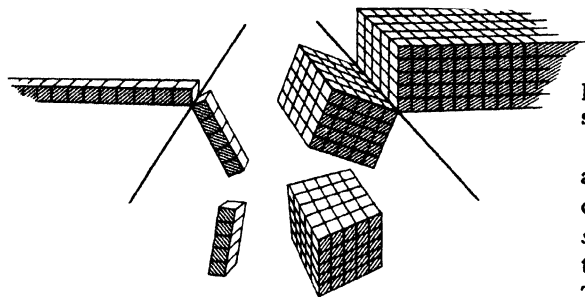


Fig. 10. Cohesive force determines the size limit of drops of a fluid. Let these cubes represent magnets, each with sufficient magnetic force so that five may cling together, but no more. A rod composed of such magnets pushed over the edge of a table will break as indicated. A thick rod will produce segments no longer than a thin one. A still thicker one would fall apart laterally and produce segments no larger than the large ones shown. This is why drops of water do not grow as large as buckets.

came back to earth, we would feel the same force again, though in the opposite direction. It is this force which makes it easier to push a moving car than to start it going, or to stop it again once it is moving.

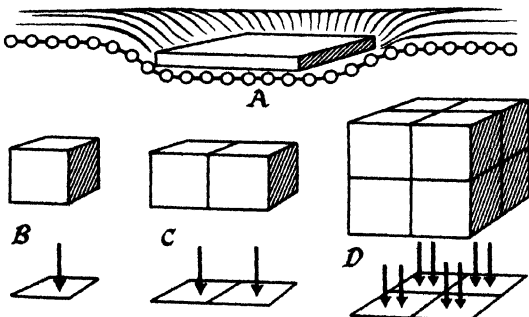
Cohesion and Adhesion

Not only do separate bodies of matter attract each other, but the bodies themselves are held together somehow, and we may inquire a little into the forces by which this happens. Fundamentally, these are two, *cohesion*, the attraction of molecules of the same kind, that is, microscopic units of the same substance; and *adhesion*, the attraction of molecules of different kinds. If, in the rocket out in space, we were to try to pour a glass of water from a carafe, it should hardly be surprising if the water refused to pour, though we might get some of it out by jerking the bottle backward quickly enough so that the inertia of the water would leave it behind the bottle. If we managed to do this, the water would not fall, but would hang in the air, a quivering, lucent mass assuming more or less the shape of a sphere. This could be divided and subdivided into many smaller spheres, but each time the separate parts would again take on their spheroid shape. It is cohesion that causes this to happen. The pull of every molecule, every unit of matter on every other, draws them all into the closest

possible relation to one another, and this is the shape of the sphere.

Cohesion of the molecules at the surface of a body of water or other liquid creates a peculiar elastic, membrane-like effect known as *surface tension*. Fill a glass of water just above the brim, and the surface will form a mound. This is caused by surface tension. A clean sewing needle, even though made of steel which ordinarily does not float, will do so if placed slowly and carefully on the surface of a glass of water. Each particle of water, each molecule, attracts the others near it, and those at the surface cling in an unbroken layer. If the force that tends to separate them is weaker than the force of their attraction for each other, this film will not be broken. It is this cohesive force that enables water insects to stroll about on the surface of ponds and lakes without wetting their feet. It assists in drawing ink into a blotter and oil up the wick of a lamp, and it helps to supply trees with water and mineral foods. It enables a liquid to form into drops, though its relative weakness limits the size of the drops so that they cannot, for instance, become as big as buckets. If the combined weight of all the molecules of water hanging together in one drop is greater than the cohesive force holding them to the main body of water, they will separate from the rest (Fig. 10). Under uniform conditions, all drops of water have

Fig. 11. Surface tension. A. Surface molecules of water cling despite the weight of the square plate tending to push them apart. B. A single small cube exerts a unit pressure equivalent to the surface of the bottom of the cube. C. Two cubes side by side give the same total pressure per unit area as one. D. The larger cube has eight times the volume of the smaller one, but its base is only four times larger. Hence, the pressure is twice that in B and C.



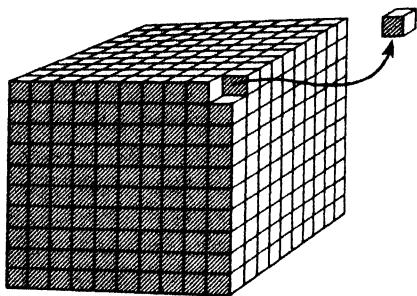


Fig. 12. Surface-volume relationship. This large cube and its smaller "offspring" illustrate the difference in surface-volume relationship that comes with size differences. The small cube has ten times as much exposed surface per cubic unit as the large one.

the same size, and that is why the volume of liquids can be measured by counting drops.

Combined with cohesion, the force of adhesion — the attraction of molecules of different kinds — is very powerful indeed for small objects. Together they make possible the rising of water in very thin tubes. Such tubes are called capillaries and the phenomenon capillarity. How powerful these forces are is seen when, for example, the wings and legs of a wet fly stick to its body as though held by glue. The fly does not have the strength to free itself from the cohesive force of the water molecules and the adhesive force of water on its body.

Indeed, these forces, which seem negligible under ordinary conditions, are tremendously potent to minute objects and creatures, and in the world of cells, the units of living substance which compose all living things, they are as pervasive and as dominant as mass, weight, and gravity are to us. If a man were the size of a dust particle — or a cell — every one of these forces would act upon him quite differently from the way it does now. In a moment we shall see how this may be, but we must first consider another set of forces which, combined with some of these, are of immense importance to living things.

Surface-Volume Relationship. Strange as it may seem, mere size is of great importance to the way matter behaves. For as size diminishes or increases, the mass of a body changes sharply in relation to the amount

of surface it has, and this change, a change in *surface-volume relationship*, affects it in a surprising number of ways. Imagine a large cube, measuring, say, ten centimeters, or about four inches, on a side (Fig. 12). Its volume will of course be $10 \times 10 \times 10 = 1000$ cubic centimeters (cc.), and each of its six faces will have a surface area of $10 \times 10 = 100$ sq. cm. The total surface area of the cube is then 600 sq. cm., so that it has 0.6 sq. cm. of surface for each 1 cc. of volume. Next, imagine that this cube is divided into separate smaller cubes, each measuring only 1 cm. on a side. The volume of each small cube is of course 1 cc., and its surface area is 6 sq. cm. Thus, where the original large cube had but 0.6 sq. cm. of area for each 1 cc. of volume, the small cube has a surface of 6.0 sq. cm. for each 1 cc. of volume, or ten times as much. What an enormous increase of *relative* surface as size diminishes!

The amount of surface relative to the amount of volume in a body is of great importance to its behavior, and this explains why a "stone" the size of a dust particle would not drop but would float in the air. Because of its greater surface in relation to its volume, a feather ordinarily falls very slowly. But the feather will drop much faster if its area is reduced by rolling it into a tight ball. Tons of wood and metal can be made to fly like a feather if the mass is shaped to have a relatively large surface.

But the surface-volume relationship has another effect on living things, perhaps even more important than all this. Organisms are largely made up of water, and water contains dissolved oxygen, a gas which is necessary to life. In large animal organisms, with a large volume in relation to their surface, various devices, such as gills and lungs, have been evolved by which oxygen is brought in, though very small creatures simply absorb it, generally from the water or moist surroundings in which they live. Without moist surroundings, such creatures would quickly dry up, since the water of which they are largely composed would evaporate. Larger land crea-

tures have evolved skins which help to protect them from this evaporation, though as anyone knows who has spent a hot day on a desert, the amount of water one drinks to replace what is lost is likely to be far greater than one's normal intake.

To try to visualize some of these things, imagine a person standing on the sand at the edge of a pond, then shrinking to about $\frac{1}{250}$ of an inch. As he shrinks, the treetops fade from sight, the pond becomes a sea, the sand becomes a plain of boulders, each over a thousand feet high — and he is standing on one of them. He tries to walk, but the air would seem thick, almost fluid, as if he were walking in water. At the edge of his boulder, he tries to drop a stone to test the depth of the pit, but the stone floats in the air until a gust whisks it away. He may find that he stops breathing, because he is absorbing all the oxygen he needs for his reduced volume through his skin. But he becomes intolerably thirsty, since his increased relative surface loses moisture at many times the normal rate. Actually, he would become a desiccated mummy, but we may compromise by assuming that he is merely thirsty. Reasoning from the behavior of the stone, he figures that he too can float down to the water to get a drink — and he does. But try as he will, he cannot break through the tough surface membrane of the water, on which he slips and slides as on elastic ice. So he comes ashore again and finds a mountainous dewdrop which he tries to pierce with a straw. If he succeeds in doing so, the water might at once suck the straw and the man into its crystal interior, holding him helplessly captive, too weak to cope with molecular forces. But it is quite likely that he would be able to carry on sufficient respiration through his skin so that he would probably not drown — for drowning is death by suffocation — even if he could not breathe.

All these new relations make it very clear that the activities of minute organisms, as of the minute structural parts of large ones, must be accomplished by methods quite different from those successful in larger creatures.

Units of Substance

We have said that living substance “absorbs” oxygen and that water “evaporates.” To see something of the nature of these phenomena, we must now look into the structure of matter, the units of which it is made up, and the forms it may take. Most obviously, it may be in the form of a *solid*, like wood or bone; a *liquid*, like water or blood plasma; or a *gas*, like the air we breathe. Many substances appear in all these forms, even in the range of temperature within which living activity goes on. For example, water may appear as ice, water, and water vapor. Whether matter is in one of these forms or another, it is never homogeneous, never a uniform, structureless mass. Any sample of it consists of unbelievably tiny units, called *molecules*, made up of still smaller units called *atoms*, which are all basically similar in structure (though with extremely important differences) and in turn are composed of still smaller particles. Different kinds of atoms group themselves in varying combinations to form an almost unlimited variety of molecules and substances.

Solid, Liquid, and Gas

Let us try to visualize some of this. Suppose you were reduced to the size of a dustmote, $\frac{1}{250}$ of an inch. A speck just visible at your reduced size would be $\frac{1}{15,000,000}$ of this size, or $\frac{1}{250}$ millionth of normal human size. If one could be this size, he might see atoms the size of baseballs though not so solid. Imagine thus standing on the edge of a dish containing a lump of ice, somehow immune to the violent action all about.

The dish — a solid — is a mass of clinging, quivering spheres, ranging in size from baseballs to watermelons, vague in outline yet tightly packed into organized groups that repeat the same pattern over and over. In the valley below, the ice is a mountain of more such spheres, though these are all of the same kind, and each consists of two smaller spheres interlocked with a larger one. These also remain in position, for ice too is a solid.

But at the base of the mountain is matter in a different form, a liquid, formed by the melting of the ice. Here the molecules — the same kind as those in the mountain — are no longer in fixed positions, but slide past each other in a squirming, level mass. Finally, whizzing through the “air” all about are still more atoms and molecules. These differ from those in the mountain in size and in their wider spacing and greater freedom of motion, for this is a gas. There are constant violent collisions and elastic reboundings between molecules on all sides. As speeding air molecules strike sluggish ice molecules, the latter become more violently agitated, and some lose their fixed position to slide into the valley below. As some of the faster air molecules strike the liquid, they dive in and remain there — they go into solution and diffuse.

Heat and Cold

Intense motion of molecules produces the phenomenon called heat, and slower motion produces cold, which is simply the absence of heat. Thus the ice molecules move most slowly, those in the water next, and those in the air most rapidly. When the faster air molecules strike the slower ones in the ice, some of the energy of their motion is transferred to the molecules in the ice, with the result that the latter speed up — take on more heat — and some of the ice melts. As some air molecules enter the water, and as others strike it and rebound, some of their energy is transferred to the water, which becomes more agitated — and becomes warmer at the same time that the air becomes cooler. Here and there the movement of the water molecules becomes great enough to lift many of them above the common level. They leap from the main mass into the air, only to fall back again. But as more and more energy is transmitted from air to water, some of the water molecules finally break away from the main body, and mingle with those of the air. This is evaporation and the subsequent diffusion of the evaporated water molecules into the air. In the

meantime the mountain of ice has disappeared, as molecule after molecule became sufficiently agitated to break its bond. More and more water molecules leap into the air and are off, because of their greater than average speed, imparted to them by fortuitous collision with other water molecules. The average speed of those left behind is lowered. Thus solid, liquid, and gas can be interchangeable, depending on the energy — the heat or cold — which the molecules possess. Their mutual attraction tends to hold them together unless some stronger force causes them to separate. But if they are given sufficient energy of motion, the molecules in solids will separate to form liquids or gases.

Kinetic and Potential Energy

All the activities of matter — and that includes all living things — are expressions of some form of energy. Energy is generally defined as the “capacity to do work,” that is, the ability to cause matter to alter its direction or degree of motion. Actually the relationship between matter and energy is much more intimate than this statement implies.

Energy may manifest itself on a number of different levels; and by various means one form of energy may, at least partially, be converted into any other form. Energy may be classified according to the forms of matter involved: there is the *movement of visible bodies*, such as a bird flying through the air; the random movement of molecules within a portion of matter, which manifests itself as *heat*; the movements involved when atoms within molecules change their relative positions and patterns, as in the digestion of foods which is called *chemical reaction*; the flow of particles called electrons along a conductor, as in a perve, which is called an *electric current*; or the transmission of units called photons, as in a ray of *light*. All these are forms of energy, and all, within the limitations of certain laws, are interconvertible. But all of them are classified as *kinetic energy* (Gr. *kinein* = to move).

Particles may, however, also contain energy

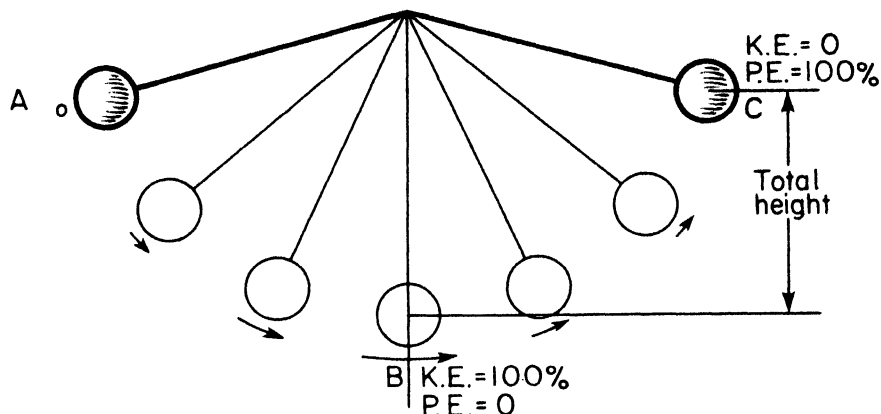


Fig. 13. Potential and kinetic energy. At A, before it starts down, the pendulum has its maximum potential energy. As it drops, potential energy decreases to zero at B, while kinetic energy or speed increases to 100 per cent. The vertical distance from A or C to B is a measure of the total available potential energy. Arrows indicate relative kinetic energy at given points.

in a form not obviously manifest as motion, though the division is more or less arbitrary. Such energy in apparently inactive form is called *potential energy* (L. *potens* = being able, powerful). Potential energy may be due to position, such as the energy in a pendulum at the height of its swing (Fig. 13).

Potential energy may also be present in the form of attraction between molecules, whatever the nature of this attraction may be, as in cohesion and adhesion. This may become kinetic energy, as when liquids rise in the capillary vessels of a tree. Or atom may attract atom within a molecule, causing a tension which upon release may manifest itself as movement, as in the contraction of a muscle fiber. Atomic attraction may also result in a chemical reaction which may cause an increase in the vibration or speed of the entire molecule, thus transforming the potential energy of chemical affinity into kinetic energy of heat, as in the rapid utilization of sugar.

Such transformations underlie all happenings that affect our senses, and always involve a change in the motion or structure of some particle of matter. Change in structure always involves motion, and all events consist of energy transformations. Thus life, whatever

else it may be, is indisputably a series of events, of energy and matter transformations (Fig. 14).

Two Laws of Energy

All energy transformations are governed by two simple laws. Consequently, these two laws are the fundamental laws that govern the nature of life itself. The first is the law of *conservation of energy*, which states that in any energy transformation the total quantity of energy remains unchanged. This means that however many times energy changes or is transformed — as from light to chemical change to heat — the total amount released, as in the utilization of a food, is exactly equal to the amount absorbed in the process of its creation. The wastes left have little energy remaining in them, for what energy has not been used by the body has been transferred to the air. But no energy has actually been lost. It still exists elsewhere, and in some form it always will.

The second of these laws is the *law of degradation of energy*, which states that heat appears to be the ultimate end of all energy transformations, and that all forms of energy may be entirely transformed into heat, but that heat may never be completely transformed into

other forms of energy. Thus, in transforming the energy in food into work, considerable quantities are lost as heat into the surrounding air. Much of this loss is due to imperfect efficiency, but according to this law, it is theoretically impossible to create either a machine or a living organism that will utilize all the energy of the fuel. It is not too difficult to see why. Heat has been defined as the *random* movement of molecules, which rebound when they collide, since they possess the property of perfect elasticity. After such a collision, the sum total of the speeds of the rebounding molecules is the same as it was before the collision. If one is slowed down, another will gain in speed exactly what the first one lost. If, for example, a cold hand is put into hot water, the rapidly moving molecules of the water will strike the more slowly moving ones of the hand. The slow ones will be speeded up, the fast ones slowed down. Or, in everyday language, the hot water will become cooler, the hand warmer. Eventually, a point will be reached when the average speed of the molecules in both will be the same, and when this happens no further energy transfer will be possible. Some of the energy originally in the warm body will have to stay there. It is impossible to "draw out" all the energy from the

one body and transfer it to the other, for a warm body cannot be further warmed by one that is cooler.

Moreover, compression of a gas causes a rise in temperature, because the more crowded molecules collide more frequently. This increased molecular motion is heat. Similarly, expansion of a gas lowers its temperature.

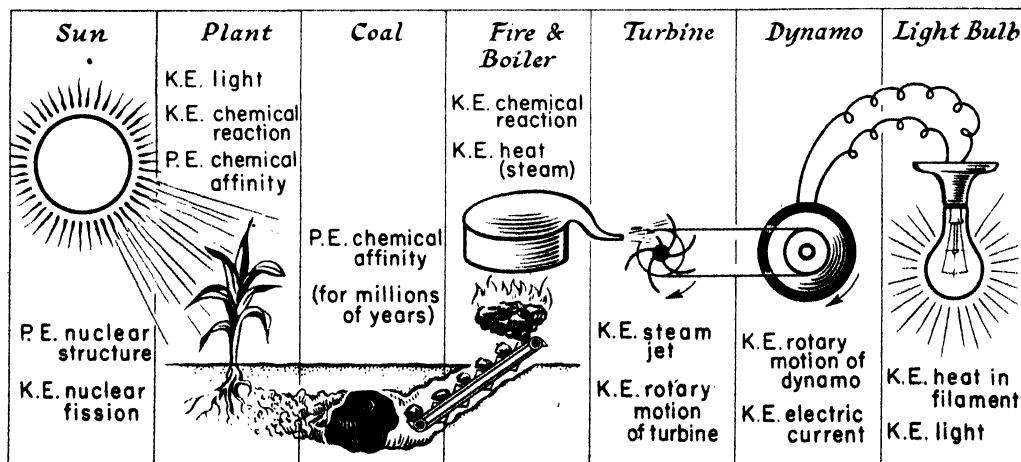
Friction also produces heat, as any one knows who has rubbed his cold fingers to warm them. When the molecules of one body strike or rub against those of another, these will be speeded up.

Life and the Behavior of Matter

All these principles apply to the study of life. Thus it should be clearer why sweating cools, why we get thirsty, why minute organisms live in a liquid, how body temperature is maintained by transformation of chemical energy in foods, and how the food obtained its potential energy through sunlight falling on the plant which produced the food.

It should also be clear that the size and shape of the earth is responsible for the form and shape of the life upon it, though the relationships here are involved. Since the mass of the earth determines its gravity, its size and composition also determine the quantity

Fig. 14. Energy conversions.



and quality of our present atmosphere. Temperature conditions of the past and present controlled the kinetic energy of the gases that form the atmosphere, and this, influenced by the mass of the earth, determined which gases would remain near the earth and which would be lost in space. Since the smallest or lightest molecules have the greatest speed, these escape much more readily than the heavier ones. Thus earth has lost most of the hydrogen atoms that were once in its atmosphere; only the heavier oxygen and nitrogen molecules remain. This appears to be fortunate for us, since otherwise our atmosphere would consist largely of marsh gas (methane, CH_4) and ammonia (NH_3), as appears to be the case on such giant planets as Jupiter. Both these gases are intensely poisonous to living creatures as we know them.

If, on the other hand, the earth had as little mass as the moon, all the gases would have escaped — or would never have been captured — and there would be no atmosphere and probably no life. In short, life is what it is because matter behaves as it does, and because, through a fortuitous set of circumstances, the principles which govern matter have conspired to make life possible.

THE STRUCTURE OF MATTER

The Forms of Matter: Chemical Change

Although matter may be transformed more or less readily from one *physical* state to another, it is less easy to transform it from one form into another. Thus water, the chief component of living things, remains water under all sorts of physical conditions, whether as a solid, a liquid, or a gas. It is possible, however, to subject water to such treatment that it changes its characteristics completely and ceases to be water at all. Such a change is called a *chemical change*, and changes of this kind are the very essence of living substance.

A simple chemical change can be achieved by passing an electric current through water. Bubbles will rise from the conducting electrodes and the water will gradually disappear as gases are produced. These gases are not

water vapor, or steam, as their behavior will clearly prove. Experiment shows that the two gases produced at the opposite electrodes are quite different from each other and quite unlike the water from which they clearly were produced. Like water, they are colorless and odorless, but under suitable conditions they unite violently, explode, and again become water vapor. The gases thus produced are called hydrogen and oxygen, and may combine with many other substances, even as they combine with each other.

Again, sugar — the chief fuel of life — may easily be converted into carbon and gas. If ordinary corn sugar is put in a pan and heated in the presence of air, it will turn black and produce an acrid smoke. The small black residue is carbon, and the "smoke" is gas. If the heating is continued, even the carbon will disappear. The substance of the sugar has not vanished, however. There is just as much matter as there was before, though now it is in different forms. In fact, the gases produced by the burning of the sugar will actually weigh more than the sugar did. This is because something in the air was taken out of it and combined with something in the sugar to make these gases. It was the gas oxygen in the air which made it possible for the sugar to burn, and the combination of oxygen with the sugar increased the weight of the gases produced by the burning of the sugar. These gases are carbon dioxide and water vapor or steam.

It is also possible to make sugar out of these substances again, though chemists have not yet found a way of doing it profitably except as it has been done for the past several hundred million years — that is, in the leaves of green plants. This particular round of chemical changes happens to be of supreme importance to living things, because sugars are widely found in living organisms, carbon is an extremely important substance in many of the chemical compounds of which they are composed, and carbon dioxide and oxygen are gases which they constantly exchange, that is, either take in or give out. Moreover, sugar is

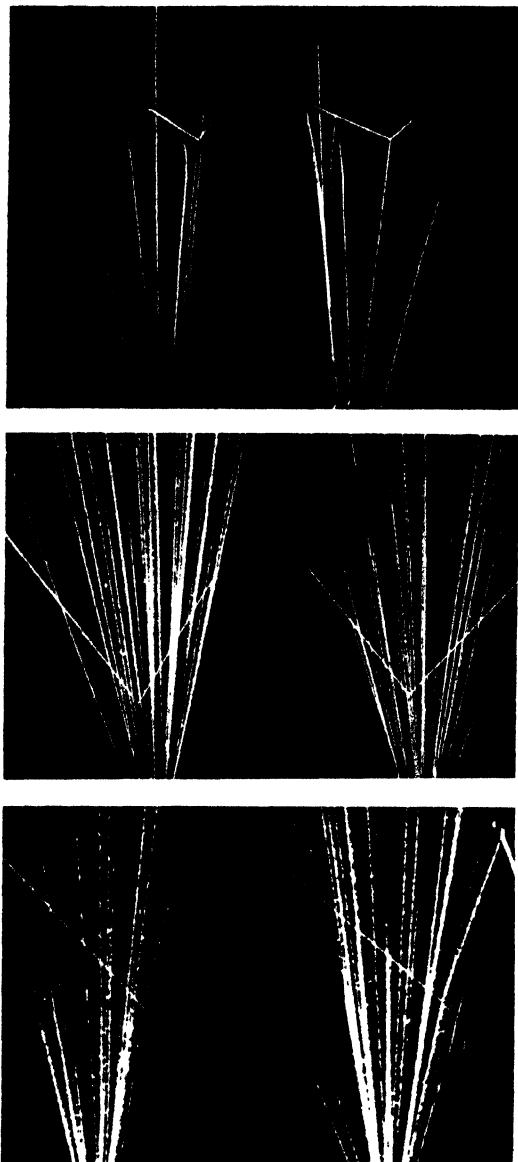


Fig. 15. Visual evidence of the existence of atoms is provided by these photographs, taken by Blackett, showing the paths of alpha particles from radium as they pass through a cloud chamber. The alpha particles collide with atoms of a gas (reading down, with oxygen, helium, and hydrogen) and knock electrons out of the atoms. The atoms then become electrically charged ions, and minute vapor droplets form around them. These make up the vapor trails. Such photographic evidence argues that atoms are composed of a heavy, positively charged nucleus and lighter, negatively charged electrons.

produced by plants and is found nowhere except as a product of plants, though they must make it out of something else, since it does not occur in the soil, the air, or the water to which they have access. They make it out of the carbon dioxide in the air and the water in the soil. It is from this sugar, together with other substances taken from the soil, that they build the various substances of which they are composed and obtain the energy which must be ceaselessly introduced into their living structures so that they may continue to live. Nearly all other organisms depend upon this sugar also, appropriated in the form of food. Thus it is only by a series of chemical changes that life is able to exist — by substances combining with others to form new ones, or separating again to recombine in an endless series of transformations.

The Elements: Basic Substances

But there are limits to the possible transformations of matter. Thus water may be reduced to hydrogen and oxygen, and sugar to hydrogen, oxygen, and carbon; but for these substances no further simplification is possible without destroying them as substances.

There are only ninety-two ordinary basic substances, or *elements* on the earth, and all the infinitely varied forms of matter we meet every day are merely combinations of these ninety-two basic forms.¹

Atoms

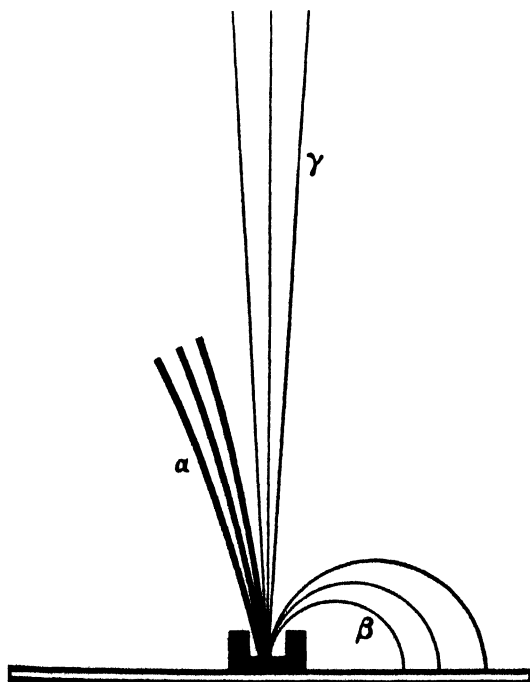
The unit particles of elements are *atoms*, which combine to form more complicated groupings called *molecules*; as the molecule of water is composed of two atoms of hydrogen and one of oxygen. Moreover, the atoms themselves have structure, and since their structure endows the separate elements with their special properties, there are only as many elements as there are kinds of atoms.

¹ Certain more or less synthetic elements have recently been added to the list, but these are at present of biological significance only indirectly by way of the atom bomb and in some biological research.

Because of their sub-microscopic size, until recently no one had received any direct sensory evidence of the existence of these units, although they had been talked about ever since the days of ancient Greece. Today, though no one has yet been able to see them in the same sense that one sees a bird or a tree, there is visual evidence of their existence that is almost as good. Even this indirect evidence is a triumph of science, for the size of these units is small almost beyond conception (Figs. 15 and 16).

Atom sizes may be expressed in centimeters (1 inch = 2.54 cm.) by the number 10^{-8} . That is an eight-place decimal figure, .00000001 cm., or as a fraction, $\frac{1}{100,000,000}$ millionth centimeter. An atom large enough to be visible to the unaided eye would have to be at least $\frac{1}{10}$ millimeter in diameter, or about one million times larger than it actually is.

Fig. 16. In a magnetic field, alpha and beta particles are turned in opposite directions, indicating opposite charges. Alpha particles, with greater mass, are deflected less than the lighter and more highly charged — as related to mass — beta particles. Gamma rays are not visibly deflected.



ATOMIC STRUCTURE

As a result of experiments in the shattering of atoms, physicists know that atoms consist of still smaller particles. Physicists have counted, weighed, and measured the electrical charges, and clocked the speeds of such particles, and they have made various more or less successful attempts to construct models that show how these particles are arranged to form an atom.

Miniature Solar System

In many ways an atom is similar to a miniature solar system, except that the number of smaller satellite bodies which whirl about the central "sun" varies considerably and in part determines whether an atom is oxygen, for instance, or hydrogen, or carbon, or any one of the other ninety-two elements. Earlier concepts of the atom bore a much closer resemblance to the solar system than do more modern ones.

To begin with, the atom contains a relatively large central mass, the *nucleus*, which performs somewhat the same role as the sun in the solar system. Around the nucleus revolve one or more orbital *electrons*, which roughly correspond to the planets. In the earlier concepts of atomic structure, these orbital electrons were rather literally thought of as tiny, hard, planet-like bodies. In more recent thought, they have lost much of their solidity, and virtually dissolve into hazy, shimmering unrealities.

"Picture" of an Atom

If an atom could be magnified to the size of a house, it would probably look something like a great soap bubble, except that its outlines would be so hazy and indistinct that it would be impossible to tell just where the borders of the atom were. Within the misty outer shell would appear other more or less concentric or interlocking shells, each as hazy as the outer one. Deep in the center of this shimmering mass would be a denser, more solid looking structure, the nucleus, no larger

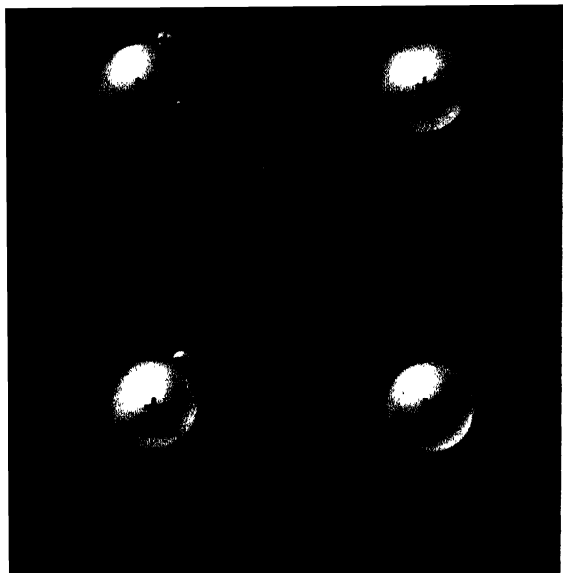


Fig. 17. Possible structure of nuclear components of atoms. If the proton (upper right) is the basic unit, a neutron would be a proton and an electron (lower left). If the neutron (lower right) is the basic unit, a proton would be a neutron and a positron (upper left). In the diagrams of atomic structure given on this and the following pages, the neutron is taken as the basic unit of the nucleus.

than a dot. Most impressive, perhaps, would be the vast emptiness of the atom, a characteristic which it shares with all the universe around it. It is strange indeed to realize that man and all living things, the earth, and all the universe are constructed of such empty and seemingly fragile structures. It has been estimated that if all the atomic constituents of the human body could be packed together tightly, eliminating the spaces between them, they would be no larger than a grain of sand.

The planetary electrons which revolve around the nucleus must be visualized as endowed with a smashing, driving energy. Even in this house-sized atom, they would revolve in their orbits with such inconceivable speed that they would not be recognized as separate units, but would give the illusion of thin, transparent shells, as unreal as the disc described by the whirling blades of an electric fan. If their speed could be reduced so that they could be made visible, they might become

vaguely outlined and intensely vibrating "objects" no larger than pinpoints, not solid, but rather, says modern physics, whirlpools of energy, foci of energy, or similar intangible units.

This is the atom as we see it today. It is probably a poor picture, and certainly an incomplete one, but it is perhaps as close an approximation of the truth as can be attained by describing in the gross terms of the physical senses; a structure beyond the range of sight. Perhaps even more surprising than that atoms can be shattered is the fact that they possess such extraordinary stability or resistance to change.

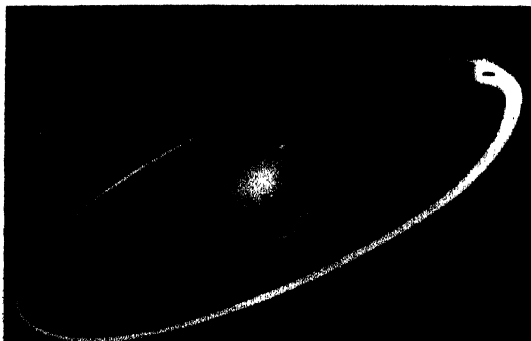
It is not easy to think of ourselves as mostly empty space, but the evidence can mean nothing else. When a person is exposed to X-rays, most of them go right through without hitting anything at all.

Particles Composing the Atom

Basic Units. The central mass or nucleus of the atom consists of particles smaller but much heavier than electrons. These are called *neutrons* and *protons*, respectively uncharged and positively charged particles (Figs. 17 and 20).

Thus matter appears to be electrical in nature, or at least electricity appears to be a fundamental quality of it. In the nucleus of an atom, protons and neutrons form a dense cluster, held together by close-range intra-

Fig. 18. Hypothetical representation of the hydrogen atom: a neutron and a positron (a proton) form the nucleus; there is a single orbital electron. If drawn to scale, the orbital electron would be about 300 feet from the nucleus.



atomic forces not yet well understood, and these represent most of the mass of the entire atom. Moreover, each nuclear proton has the power of holding one of the whirling planetary electrons in its orbit around the nucleus. Hence the number of orbital electrons is determined, in general, by the number of positive charges within the nucleus, and the atom as a unit is neither positive nor negative in charge, but neutral (Fig. 19).

The "Behavior" of the Atom. The resulting behavior of the atom — the physical and chemical characteristics of the element it represents — is determined largely by the number and arrangement of the orbital electrons. Thus the structure of the nucleus indirectly determines the nature and behavior of the atom. Oxygen is oxygen and behaves as it does because the nucleus of the oxygen atom contains eight protons, which in turn hold eight electrons in their orbits (see Fig. 20).

As a matter of fact, there are usually several different nuclear combinations that will hold a given number of electrons in their orbits. An atom may have one or several neutrons more or less than the usual number, but as long as the number of positive charges within the nucleus is the same, there will be no change in the number or arrangement of orbital electrons. Such an atom will have the same chemical characteristics as those of its kind with the more usual number of neutrons, but its atomic weight will differ. Such variants are called *isotopes*. Because of their differences in weight

Fig. 19. On the assumptions of Fig. 17, the helium atom would contain two neutrons and two protons — each proton a neutron and a positron. There are two orbital electrons.

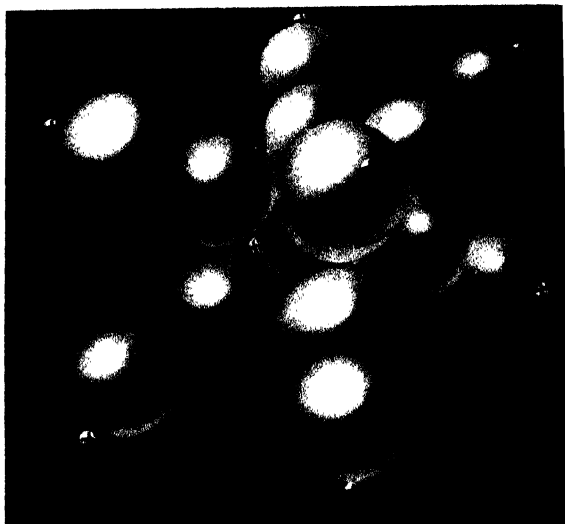
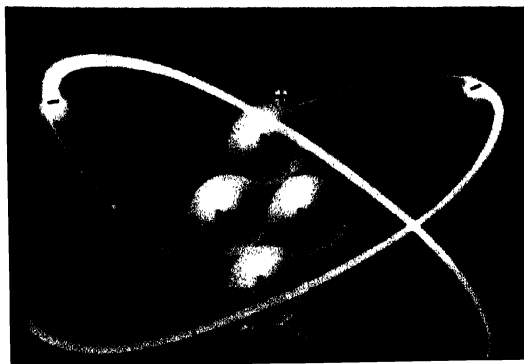


Fig. 20. We may imagine the oxygen nucleus to look somewhat like this, with eight neutrons packed together and eight protons grouped around them. Orbital electrons would have to extend out about 1000 times as far from the nucleus as shown in Fig. 18.

or radioactivity from the more common forms of the same elements, these isotopes can be used as chemical tracers in the biological processes of living organisms. They are at the present time spectacularly increasing our knowledge of the chemistry of life.

The Periodic Table (in Part)

The ninety-two basic kinds of atoms are built according to a scheme as precise and orderly as if it had been designed by a mathematician. It is therefore possible to arrange them in a series, known as the Periodic Table, according to the increasing number of their protons and orbital electrons. The pattern upon which all atoms are built can be illustrated by a simple diagram (Fig. 21), consisting of a central core, the nucleus, around which are seven concentric circles, representing the electronic orbits or shells from K through Q. Each orbit has a number attached to it, indicating the maximum number of electrons it can accommodate. As a general rule, and always in the smaller atoms, an inner ring must be filled before a second appears. Thus an atom may have two electrons on the first (K) ring and one or more — up to eight —

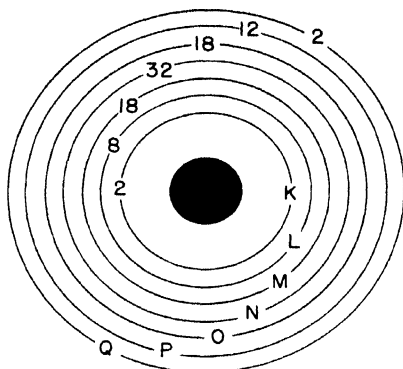


Fig. 21. The atom scaffold. (See text.)

on the second (L) ring. However, if it has only *one* on the K ring, then it can have *none* on the L ring. Iron (Fe), which occupies the twenty-sixth place in the list of elements, is here shown out of its correct position (Fig. 22).

Atomic Weight

The atoms are arranged according to the number of their planetary electrons, and thus also according to the number of protons in their nuclei, since it is the protons which retain the electrons in their orbits. The atoms are thus arranged in the order of their increasing *atomic weight*, which is determined by the number of **protons** and neutrons in the nucleus. Hydrogen, with one proton and one electron, is arbitrarily assigned the weight 1. Helium, the second element on the list, with two orbital electrons held by two nuclear protons, thus would be expected to have the atomic weight of 2. But in addition to its two protons it

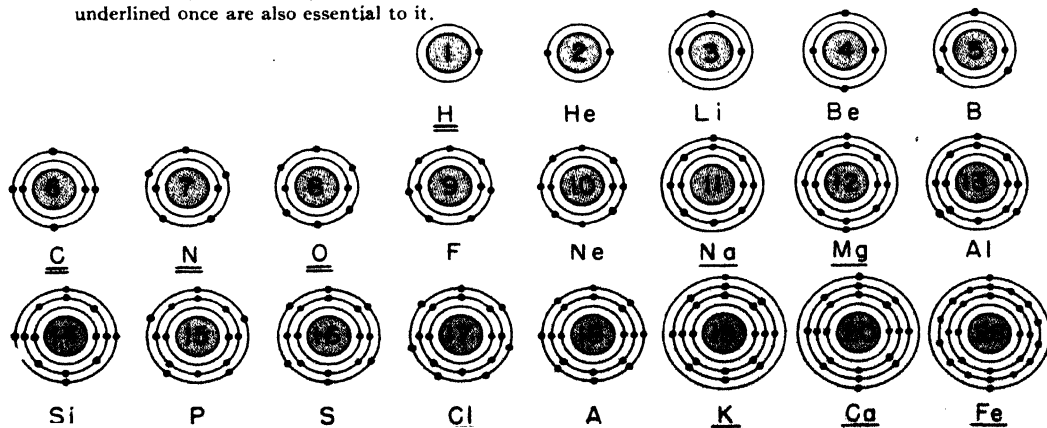
also has two neutrons in its nucleus, so that its atomic weight is actually 4. The atomic weights are relative rather than absolute, for it is not possible to weigh a single atom as we would weigh an apple or a potato. Chemists can only weigh equivalent quantities of atoms and thus compare the weight of the atoms of one element to those of another.

How Atoms Gain or Lose Electrons

Atoms with less than half the maximum number of electrons in the outer ring may under certain conditions lose those they have. Atoms with more than half this number may gain other electrons until the orbit is filled. Since such losses or additions are confined to the orbits and do not affect the structure of the nucleus, the atom can no longer be electrically neutral after such a change. Within each atom protons and electrons are exactly balanced to begin with; thus any change in the number of orbital electrons gives the atom an electrical charge — positive if it loses electrons, negative if it gains them.

Such charged atoms are called *ions*. Those which have lost electrons and are left with excess positive charges in the nucleus are called *cations*. Those which have gained electrons are called *anions*. Since unlike charges attract and like charges repel each other, cations combine with anions. The proportion in which atoms may combine is determined by the number of electrons on the outer orbit to begin with and the number that can be lost

Fig. 22. Section of the Periodic Table. The atomic number of each element is given in its nucleus. Electrons are indicated in their respective orbits. Each vertical column represents a family of elements, except that iron (Fe) is out of place. Note that with K a new orbit begins, though the M orbit is not full. Elements with symbols doubly underlined are the four predominant in the composition of living matter; those underlined once are also essential to it.



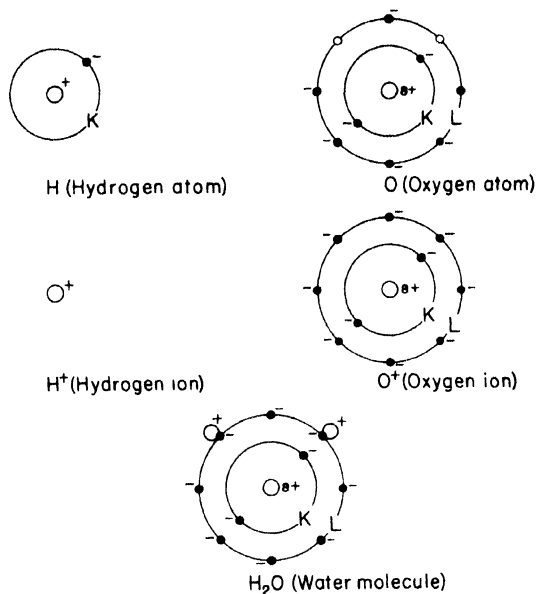


Fig. 23. Formation of a molecule of water from an atom of oxygen and two of hydrogen. Only one atom of hydrogen is shown in upper part of diagram.

or gained. For example, since hydrogen has only one electron, it tends to lose it, becoming a cation. But oxygen, with six electrons on the outer orbit, tends to gain two more to complete the ring, becoming an anion. Thus oxygen and hydrogen readily combine with each other. Since hydrogen loses only one electron and oxygen gains two, two atoms of hydrogen tend to combine with one atom of oxygen. The resulting compound is water.

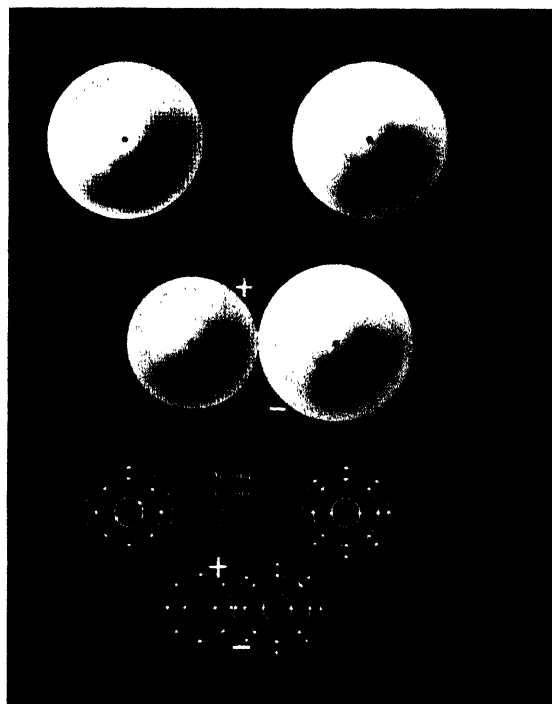
Molecules and Ions

Although atoms are the smallest particles of elements that combine to form substances, the smallest portion of a substance that can exist alone is the *molecule*, a grouping of interlocked atoms. Molecules vary greatly in complexity, ranging from the simple water molecule to the immensely long carbon chains and rings found in many living substances. They may contain atoms of only one kind (O₂), in which case they become molecules of that element; or they may contain atoms of two or more different elements (H₂O), in which case they are molecules of a *compound*. Atoms are "drawn" and held together in molecular patterns by valency, either by the attraction

of ions, or by the sharing of an electron by two different atoms.

Since living organisms are so largely water, there are many substances soluble in water that are present in them chiefly in a dissolved condition. In solution, many of these dissociate to form ions. For example, when a molecule of common salt, that is, sodium chloride (NaCl), as characteristic of blood and plant sap as it is of sea water, dissolves in water, it readily dissociates into an electropositive sodium ion, Na⁺ and an electronegative chlorine ion Cl⁻. The sodium atom has lost its single outer valence electron (Fig. 24), and the chlorine atom has gained one extra valence electron, filling the one vacant position in its M ring. Substances which dissociate to form ions are classified as *electrolytes* and *polar substances*. They are called electrolytes because they have the property, by virtue of the charges which they carry, of conducting an electric current. They are called polar substances because the ions

Fig. 24. Sodium chloride molecule. Sodium atom at left, chlorine at right.



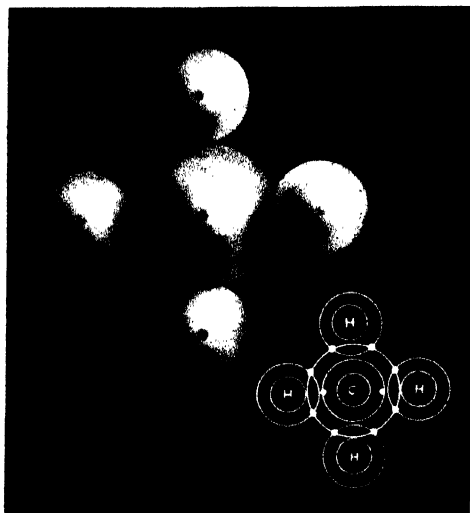


Fig. 25. Methane molecule.

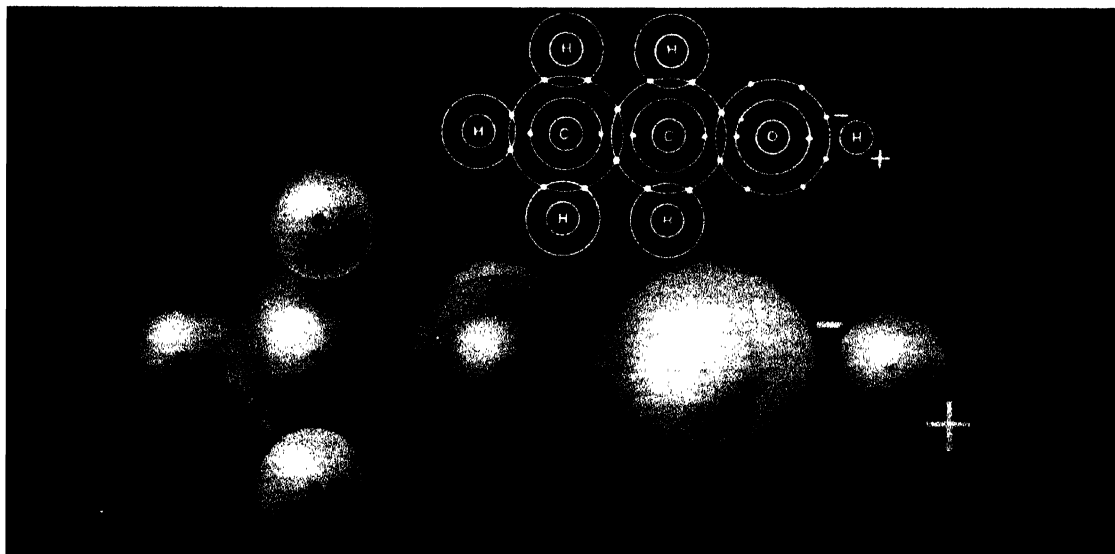
of which they are composed form two poles, with the negative ion at one end and the positive at the other. Even when the ions unite, positive with negative, their polar qualities are not quite eliminated, and they show certain characteristics, such as increased attraction between their molecules, that differentiate them from non-polar compounds.

Acids and bases (alkalis), as well as salts, form ions in solution. The acids characteristically produce hydrogen ions, H^+ ; the alkalis

characteristically produce hydroxyl ions, OH^- . The presence of ions derived from salts is of great importance to life, but the balance of hydrogen and hydroxyl ions is of still greater significance, for life can exist only when the hydrogen and hydroxyl ions are very nearly equal in abundance. In other words, organisms are killed by any great departure from neutrality, either in the acid or alkaline direction.

The atoms in a molecule of salt are held together through the attraction of the positive and negative ions for one another. Another sort of combination of atoms into molecules is by sharing electrons rather than gaining or losing them, the atoms being held together by the electrons mutually shared. Thus carbon (C) and hydrogen (H) combine to produce CH_4 — methane or marsh gas — as well as a host of compounds (Fig. 25). In this molecule each hydrogen atom shares its electron with the carbon atom, making available to the carbon atom the four additional electrons it needs to complete its outer ring and achieve a stable configuration, while the carbon shares one of its four electrons with each of the four hydrogen atoms, thus providing each of them with the additional electron it requires. As a consequence, no ions are formed and the symmetrical arrangement of the hydrogen atoms around the carbon atom produces no polar effect. The compound is *non-polar*.

Fig. 26. Alcohol molecule.



Some substances show a combination of these two methods of forming molecules. In alcohol — consisting of two linked carbon atoms, one oxygen atom, and five atoms of hydrogen (Fig. 26) — all the bonds between atoms are by sharing electrons save for one. Linked to the oxygen is a hydrogen ion, held by the attraction of opposite electrical charges. Thus the carbon-hydrogen end is typically non-polar, while the oxygen-hydrogen end is polar. Such molecules are a very common type in living substance, and their dual nature plays an important role.

The Carbon Atom

Of all the lighter atoms, only carbon — and to a lesser extent silicon — is able to combine with other atoms of its own kind, as carbon with carbon, and extensively with atoms of other elements at the same time. This ability results in the formation of immensely long chains and rings of carbon atoms, to the links of which may be attached many other atoms of various kinds, both electronegative and electropositive. It appears that carbon possesses this ability because it has exactly one half the maximum number of electrons in its outer orbit and thus tends neither to lose nor to gain electrons, but to share them in covalency. It will at once be apparent that this makes possible the formation of an almost unlimited variety of the most complex molecules with widely differing properties. A mixture or system containing such molecules combines a variety of characteristics and a versatility of reaction equaled by no other system. For this reason, carbon substances are complex and variable enough to meet the requirements of a basic life material. Furthermore, these complex carbon compounds are found today only as products of the activities of living organisms — and living things are composed largely of them. Such compounds are called *organic compounds*.¹

¹ It is to be noted that not all compounds which contain carbon are termed organic. Also, modern chemists are now able to synthesize many organic compounds.

CHEMICAL CHANGE AND LIFE

Chemical Change in Organisms

So far as life is concerned, the formation and disruption of compounds has two basic results. They are, first, the creation of the structure or organization which constitutes the living substance; and second, the conversion of energy from one form to another, of which all the life processes consist. Briefly, the formation of compounds which, because of their structure, can function and change so as to produce the orderly flow of energy which is necessary to life, maintains the living organism and gives it the power to produce further life, that is, to duplicate itself.

Energy released by the conversion of one compound into another may be employed to build up other structural compounds. It may be transformed into the physical energy of increased molecular motion (heat), or into the orderly movement of molecules resulting in motion within the organism, such as the contraction of muscles or the beating of fine hair-like processes called cilia, found in many animal organisms. Again, energy released by the conversion of a compound may be utilized to transfer electrons from one compound to another within the living substance, thus building up electrical charges. Where these are cumulative or progressive, they may assume the characteristics of an electric current, as in nerve impulses or in the electrical charges of the electric eel or the torpedo. And finally, energy released by the conversion of a compound may be converted into light, although only a few organisms possess the power of luminescence.

Chemical change always involves a rearrangement of the electrons in their orbits or energy levels. In some changes, electrons are rearranged in a pattern representing a higher energy level, and this requires the influx of energy from other sources. In living substance, this means that food or other sources of this energy must constantly be entering the sphere of life. In other chemical changes, electrons are rearranged in patterns represent-

ing a lower energy level, and in this process energy is released. This energy may express itself in any of the various ways indicated above. The first type of chemical change — to higher energy levels — supplies the energy-rich bonds of the complex chemical compounds which make up the living substance. The second type is the source of the energy by which these substances are built.

The Source of the Energy: Sunlight

We have seen (page 27) that heat appears to be the ultimate end of all energy transformations and that all other forms of energy may be entirely transformed into heat, but that heat may never be completely transformed into other forms of energy. If this is true, then the ultimate end of the energy embodied in living substance is that it is transformed into heat and lost to living things — and life runs down and even runs out. And so it would, were it not for an ever present source of new energy which comes into it and by chemical change keeps it going. This source is sunlight. Indeed, sunlight is almost the sole driving force behind the phenomenon of life. Let us see, briefly, something of what this light is.

Like other forms of energy, light is created by the shifting of orbital electrons within the atom from a higher energy level to a lower one. According to modern theory, light (like other kinds of energy) should be thought of as merely another form of matter. It may therefore be converted into still other forms of matter, or it may be created by the conversion of unit particles of matter. We are told that light is composed of unit particles or quanta of energy called *photons*, which vary in energy inversely with wave-length.

Only photons of specific wave-lengths can be absorbed by particular atoms and molecules and thus raise the electron to a higher energy level. An atom, in turn, may use this increased

energy to combine with other atoms. Thus, under certain conditions, light may cause chemical changes of the sort by which electrons are rearranged in patterns representing a higher energy level. In chemical terms, this means that simpler atomic and molecular structures can be transformed into more complex ones rich in potential energy.

Sunlight and Life

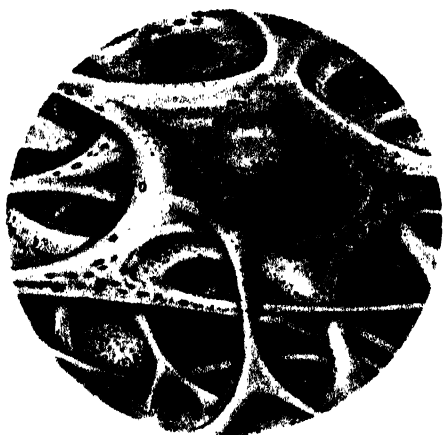
This is precisely what happens in life, through a process known as *photosynthesis*, which goes on in the leaves and some other parts of green plants. This process produces from nothing more than water and carbon dioxide the complex molecule of glucose, or corn sugar, which is the true "staff of life" for nearly all plants and animals.

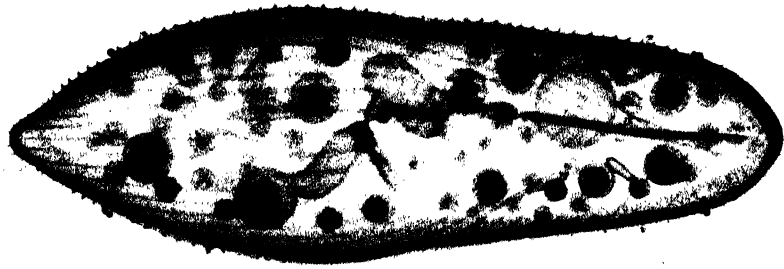
This sugar is packed with energy which can be released for further chemical changes, resulting in the formation of vastly more complex substances even than the sugar. This will be more fully discussed in Chapter 4. The important thing is that the energy of the sunlight is absorbed into the green plant by the agency of a substance known as *chlorophyll* and enters into the formation of a sugar, thus shifting electrons from lower to higher energy levels.

Thus life is a ceaseless round of chemical changes, from lower levels of energy to higher and from higher to lower, as molecules are taken in, transformed from simple to complex, broken down again, and expended from the living creature. The hand that holds this book, the eye that reads this page, and every other part of the organism to which these things "belong" is a staggering complex of whirling particles — of protons and electrons forming atoms, of atoms combining and recombining to form molecules of substances being built up and broken down again so that the hand can hold the book, the eye can see, the nerves carry impulses, and the mind receive a meaning.

PART TWO

THE NATURE OF LIFE





Life is a thing of unbelievable complexity, yet even extremely small organisms, like the one-celled animal (Paramecium) shown above, show its essential complexity.

The Nature of Life



What do we mean when we say a thing is alive? Any child knows that a dog is alive and that a stone is not. But he may not be so sure about a tree. However, with experience, one learns to tell a dead tree from a live one. What this means is that gradually, perhaps unconsciously, we establish criteria for judging between living and non-living things. We learn to expect living creatures to show certain characteristics in one form or another.

We expect living organisms to be watery in texture, never dry or powdery but always moist and generally soft, at least inside. We expect them to have a definite, complex organization of parts and structures that function. They are composed of substances often good to eat and different from metals and stones, substances of a sort that will burn. All living things, plants as well as animals, consume food, although most plants absorb theirs from the soil whereas animals eat. Then we may notice that very commonly gases from the air are also taken in, a thing not frequent in inanimate systems. Living things move, some rapidly, as most animals, others, more slowly and less obviously, as plants. The movement seems to spring from within them, rather than being simply imposed on them by external forces. The activities of living organisms appear, in other words, to be responses to stimuli they receive, and these responses are made continuously, so that the organism is always expending energy. Even in sleep or rest or apparent cessation of activity, some flow of energy goes on. A living organism is not static, but dynamic. One of the most obvious and striking features of livingness is growth, which is practically always accompanied by development, that is, a characteristic change in form and structure. Finally, it

is typical of living things to reproduce — and always to reproduce their own kinds. A cat has kittens, not pups, and its kittens not only grow up to be cats but inherit special family characteristics.

ANIMATE AND INANIMATE SYSTEMS COMPARED

No one of these attributes of life is the exclusive possession of living creatures. Non-living systems composed of liquids and solids may be soft and watery. Crystals show such definite organization that their identity may be established by counting their faces and measuring their angles, for a crystal is not a random collection of molecules but a perfectly organized molecular structure (Fig. 27).

Fig. 27. A group of quartz crystals. Living creatures are organized, but so are crystals.





Fig. 28. A chemical "garden" of salt crystals in a sodium silicate solution not only grows but shows a kind of organization.

Non-living systems may show autonomous movement (as distinct from the movement of an inert object propelled by an external force, such as dust particles blown by the wind). Witness the movement in any motor. Camphor particles, placed on water, scoot about in erratic fashion like water skaters.

Practically any inanimate system which shows autonomous movement also illustrates irritability and responsiveness. The camphor particles modify their movements in response to external changes. Slight changes in the adjustment of the carburetor cause a motor to speed up or slow down, to cough, spit, or "die."

Growth and reproduction — and continuity — are characteristic of crystals. Moreover, the growth of ice crystals on a window pane is quite different from the growth of a sand dune. The latter is merely a planless piling up of the same undifferentiated substance. But a growing crystal picks up from its environment only those molecules, atoms, or ions of the kind which compose it and fits these onto the pre-existing mass according to a strict pattern much as do the growing portions of protoplasm within the cell. Even a small fragment of a crystal has the power to direct the continuance of its own characteristic growth if the necessary molecules are available. Thus it also displays the principle of continuity.

Fascinating to watch is the growth of a

chemical garden (Fig. 28). Crystals of metallic salts soluble in water, when placed in a solution of sodium silicate or water glass, produce long plant- or coral-like growths, often weirdly beautiful and resembling formations found growing on coral reefs. Superficially they share with living organisms a certain organization and the ability to grow, and so may quite easily deceive the observer into considering them alive.

Since nutrition is the intake and use of raw material for growth and energy, then the intake of substances for energy in inanimate systems may be considered as in some ways similar to nutrition. The gasoline in an engine is burned to provide energy as the living organism consumes sugar to obtain energy. In both these processes a gas exchange is involved — respiration in organisms. A motor draws in oxygen through its carburetor; a man breathes in oxygen through his lungs. The motor expels carbon dioxide and other gases through its exhaust; the man exhales carbon dioxide and other waste gases through his mouth and nose. To be sure, there are important differences. The fuel in the engine does not become assimilated into its substance as does the food in man. Without fuel, the engine does not perish as man would without food, though it will cease to move until more fuel is provided.

The Candle Flame

Finally, we may profitably consider two

other inanimate systems. The first is an ordinary flame. Study a candle flame carefully (Fig. 30): near the base of the wick is a clear bluish zone, delicately edged with a more luminous blue. Above that appears a darker, rather colorless cone surrounded by a yellow luminous layer. Then comes a brilliant yellow cone. Finally, a less luminous yellow cone surrounds this one. Surely this is organization. Moreover, the structure is not static but dynamic. No part of it is at rest. Small incandescent particles flow from the wick upward into and through the various zones of the flame. The whole is no more static than a fountain or a waterfall, and like these it has shape and form. How sensitive it is to events in its environment! Dust in the air will cause it to flicker and alter its steady dynamic form. It may even be extinguished by smothering with an inverted glass.

The candle flame may also grow as the wick grows longer, or it may reproduce by kindling another flame. This may seem to be stretching the original concept, but it cannot be simply dismissed. Furthermore, the flame consumes "food," for the wax is converted into its structure and activity. This also involves a gas exchange exactly like that in the respiration of a living creature.

Is the flame therefore alive? Poets and philosophers have seen the similarity, and a flame has been described in terms of life, or life in terms of a flame. Yet the flame is not thought of as a living organism, for despite these re-

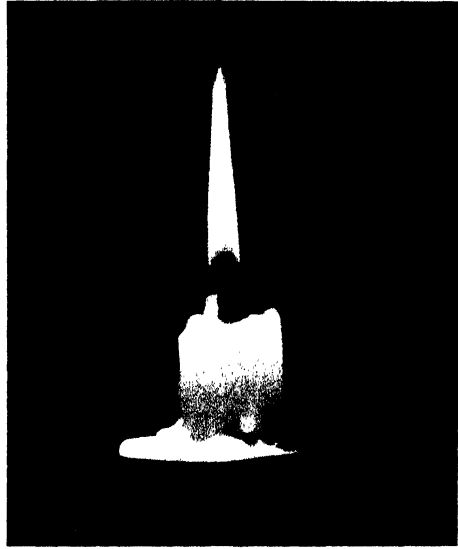


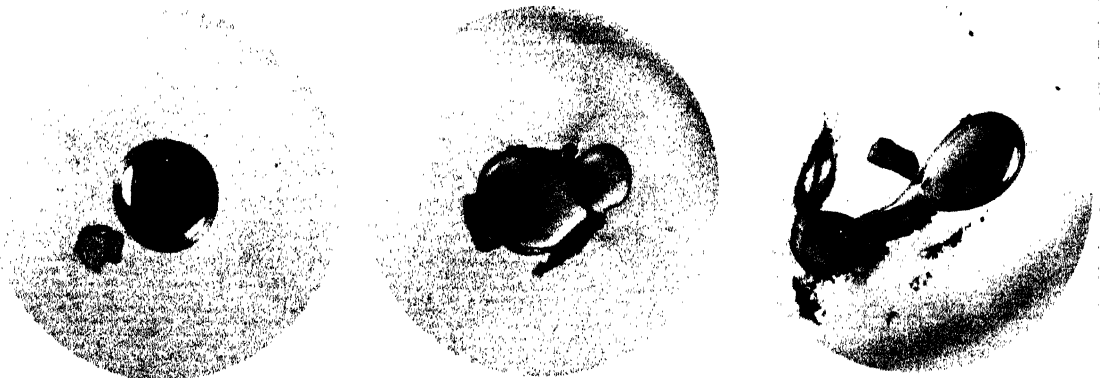
Fig. 30. Life is dynamic, but so is a flame. It also displays organization.

semblances, it is basically different from living things. Most notably, it does not have a watery texture, and it differs radically in chemical composition, for it is much less complex and its chemical activities are all destructive.

The "Mercury Amoeba"

Another inanimate system involves a simple experiment in physical chemistry (Fig. 29). Fill a small, flat-bottomed glass bowl about half full of water. Place a drop of mercury about as large as a good-sized pea in the bottom

Fig. 29. A droplet of mercury simulates amoeboid movements.



of the bowl. Add to the water a few teaspoonfuls of nitric acid. Now take a small orange-red crystal of potassium dichromate, and place it on the bottom of the dish beside the mercury. With a piece of wood — a pencil will do — push the crystal gently toward the mercury, but do not let them quite touch, for the results will be more impressive if actual contact is not made.

At first the mercury does nothing, though the crystal appears to be dissolving and diffusing, for a faint discoloration may be seen in the water surrounding it. When this reaches the mercury, sudden dramatic action begins. Swiftly the mercury droplet shoots out a tongue exactly as if it were trying to lick the crystal, but the protruded tongue is withdrawn as quickly as it appeared. A few seconds later the maneuver is repeated, but this time with more vigor and seeming assurance. The tongue-like projection actually touches the crystal, and now the mercury shows real signs of agitation. It quivers and boils, vibrates and pulses, and suddenly begins to flow towards the crystal. It is "attracted," the observer might say. But a moment's consideration will show this theory to be false, for the mercury pushes the crystal before it and may chase it completely around the edge of the dish. Meanwhile the mercury continues to quiver and boil, and clouds of an opaque, orange-brown substance are formed upon its surface. Eventually the commotion subsides. When it does, the once bright mercury droplet is completely coated with drab brown, and it lies inert and seemingly exhausted. Further acidulation and stirring of the solution will cause it to revive temporarily and the performance may be repeated.

Without knowing what objects were engaged in this peculiar dance, one might be inclined to look upon the mercury droplet as alive. It appears to show "desire" and "purpose." Until completely exhausted, it exhibits a persistent "urge" to pursue and capture the elusive crystal. It spontaneously performs certain movements and maneuvers that seem to bring it closer to achieving its "desire." In

brief, this droplet of mercury, under the conditions set up for it, simulates in a startling way some of the most obvious characteristics usually associated with living organisms. Only prolonged observation shows that it does not reproduce, though it may break into smaller globules in the heat of action; that it does not grow, or respire, or carry on nutritive processes; and that it does not show internal organization similar to that of living things.

Fundamental Characteristics of Life

We are now ready to define the basic criteria of life in a more precise and scientific manner.

1. *Protoplasm.* With the possible exception of the controversial viruses, no life, clearly recognized as such, has ever been found except as associated with protoplasm, a jelly watery in consistency, chemically complex, and highly organized.

2. *Cellular Structure.* But the organization of protoplasm goes much further than this. It is generally divided into units, called *cells* (Fig. 33), each with a central body or *nucleus* separated by a *nuclear membrane* from the surrounding *cytoplasm* which in turn is surrounded by a membrane and often also by an inert cell wall. Moreover, there are distinct structures within the nucleus and within the cytoplasm, and these change constantly throughout the life of the cell, some of them most notably at the time of reproduction. The apparent simplicity and unorganized sameness that meets the eye as we look upon living protoplasm is due only to the crudeness of our senses. It is most highly organized, and the basis of that organization is chemical.

3. *Nutrition and Metabolism.* Under these terms are grouped the many and constant chemical activities that occur within the protoplasm, the intake of energy-bearing molecules, their transformation into other more complex ones, and the breaking down of either sort for energy. Metabolism and nutrition overlap but do not coincide. Metabolism includes destructive chemical changes (*catabolism*) for purposes of energy release, as well as constructive ones (*anabolism*) in which

simpler compounds are converted into more complex ones, such as those of which protoplasm is composed. Thus the substances are *assimilated*. During these metabolic processes, the gas exchange of *respiration* and the production and elimination of waste products, *excretion*, also occur. That life is a *dynamic* process, rather than a state of being, or condition, is revealed in the never-ceasing metabolism associated with it.

4. *Autonomous Movement*. Associated with life there is always some form of autonomous movement, that is, movement from within. It is clearly and easily observable in animals, but it is no less a part of plants, although in some cases only a microscope will reveal it, as in the protoplasmic streaming within cells.

5. *Irritability (Responsiveness)*. It is in the nature of all organisms to be sensitive to environmental changes and to respond to them. This responsiveness or irritability is an expression of the labile, dynamic nature of the protoplasm of which they are composed. Even bacteria respond to chemical differences, moving toward favorable regions. Roots respond to light, gravity, moisture, and chemical influences. The retina of the eye responds to light, and nerve cells respond to the chemical stimulation of other cells. Muscle fibers respond to nerve stimuli by contracting, and thus the response of the whole organism is a composite of the responses of its parts (Fig. 31).

6. *Growth and Reproduction*. Constructive metabolism, or *anabolism*, may result in the production of more of the protoplasmic substances which compose the organism, thus

increasing its substance and its bulk. This is growth, and is a characteristic shared by all organisms. As a culmination of the growth process, all organisms are capable of producing new units of their own kind—that is, of reproduction. Although growth is ultimately essential to this process, the two are nevertheless distinct, and reproduction may be very complex. In the simpler organisms, reproduction may occur simply by a division of the protoplasm and its inclusions into two new units. In multicellular organisms, growth too occurs by this kind of division. Most multicellular organisms do not reproduce this way, however, but by a sexual process in which special reproductive cells fuse one with another and in time produce a new individual.

7. *Continuity or Heredity*. A commonplace but nonetheless remarkable outcome of reproduction is the fact that the new units show the characteristics of those which produced them. In other words, life shows a continuity of form and activity from one generation to the next in a pattern referred to as *heredity*. Obvious though this may seem today, our forebears did not always find it so. Spontaneous creation of living organisms from unorganized inanimate matter was considered a fact but a few hundred years ago.

Complexity of Life

Can these basic characteristics of life be found in inanimate structures as in living things? In principle, yes. The mercury amoeba, the candle flame, the chemical garden, and the motor all manifest some, even many, of the

Fig. 31. Movement and irritability are manifested by all organisms, even in plants. Many plants, like oxalis, raise their leaves during the day and lower them at night (the *nyctinastic* movements).





Fig. 32. A view of a microscopic world shows organization in minute living things. Bamboo-like rods are colonial algae called *Spirogyra* (3). Inside each cylindrical section is the spiral chloroplast, the nucleus and strands of protoplasm. 1. *Paramecium*, one of our most common and most interesting Protozoa. 2. *Stentor*, a large, more or less sessile protozoan. 4. *Spirostomum*. A large Protozoan with a chain nucleus. 5. A rotifer, similar in type to larvae of annelids and molluscs. 6. More common form of rotifer.

characteristics of life. But the organism combines these with a refinement and complexity not equaled elsewhere. And only the living organism achieves them all. In fact, protoplasm differs from inanimate systems as a modern aeroplane differs from a wheelbarrow. And in its intricate organization appear its most distinctive qualities. Whereas the organization of a crystal is static and inert, that of the living creature is dynamic. This dynamic nature may be compared to the form and pattern of a waterfall, a fountain, a whirlpool, or perhaps to the organized symmetry of a juggler's act with ten balls in the air at the same time. The waterfall cannot be stopped in mid-air and still be a waterfall. The juggler cannot "hold it"; the act must be dynamic or it will collapse. In the same way, life must continue as a dynamic system or come to an abrupt end in death.

The autonomous movement of a living creature usually results from a complex interlacing of chemical and physical changes unparalleled outside of life itself. The irritability of a living

creature may be analyzed into chemical and physical reactions basically like those of an inanimate system, but again the interplay of forces is so complex that a complete analysis is all but hopeless. Likewise, where growth in inanimate systems consists largely in picking the proper molecules, atoms, and ions from the environment and arranging them in a pattern about a center of organization, living organisms actually build the complex molecules of which they are composed by taking component parts of simpler molecules from their environment, disassembling them, and reorganizing them into their own kind of molecules under the influence of highly specific catalysts, substances which facilitate chemical reactions. When this action results in the creation of more molecules of an organism's own kind, it is referred to as autocatalysis. When it produces other complex molecules from simpler ones, that is, when it builds more protoplasm, the action is called autosynthesis ("self-synthesis").

Autosynthesis

Autosynthesis may be considered the unique property of living organisms, and many hold this view. Whether one accepts it or not depends on his definition of life. There is no one universally accepted definition of life, just as there can be no invariable definition of *wet*, or *gray*, or *heavy*. Yet there is every reason to accept the available evidence as indicating that certain parts of every living organism are auto-synthetic, and that these units may also play the additional role of ordinary catalysts in causing and controlling the activities of the rest of the cell or the organism. We shall meet these autosynthetic units again when we discuss *genes*. However — and it is here that uncertainty enters the definition — there are certain substances whose right to membership in the family of the animate is questionable but which still are autosynthetic. But they lack many of the other characteristics of life. They are not protoplasmic, but pure chemical substances, single giant molecules of protein. They may be crystallized without being destroyed. They are vastly simpler in organiza-

tion than recognized living organisms. So whether they are called living or non-living is altogether dubious and arbitrary. Nevertheless, autotynthesis remains one of the most distinctive features of living things.

THE PHYSICO-CHEMICAL NATURE OF LIFE

The name *protoplasm* (Gr. *protos* = first + *plasma* = form) was first applied to the living substance by Purkinje in 1840. By the middle of the nineteenth century, the understanding of life was greatly furthered by the realization that all living organisms were composed of a common substance which was responsible for their activities. The internal organization of protoplasm thus appears to be the crux of the entire problem of life. That this organization is basically physico-chemical has long been clear, but it has not been easy to analyze. Not only is protoplasm complex, but it is so delicately adjusted that the very act of analysis destroys it, so that, like a smashed watch, it no longer functions when taken apart. But also like the watch, the parts are still there, and it is possible to determine their chief chemical constituents.

View of Protoplasm

Place under the low power of a modern microscope a fragment of any plant or animal tissue, and the first thing to strike the attention is the fact that this superficially more or less homogeneous living substance presents a mosaic pattern. The units of this mosaic are the cells. Within these cells lies the viscid protoplasm.

Look first into a cell in the green leaf of a common water weed, *Elodea*. Its leaf, though small, looks much like any other leaf, but through the microscope it has much the appearance of a road constructed of transparent plastic cobblestones. As the magnification is increased, the cobbles look like hollow glass blocks, each with certain structures locked within it (Fig. 33). Lining each block is a thin layer of a sticky granular stuff. Within this, the inner portion of the cell appears to



Fig. 33. Single leaf of *Elodea* on microscopic slide.

be filled with clear water. Sailing along in the sticky lining material of the cell are green objects shaped like flattened spheres. These are called *chloroplasts*, and while important, they do not particularly concern us now. Rather, the sticky substance in which they are sailing is the goal of our attention. That is the protoplasm of the cell, and as often in plants, it does not completely fill the structure.

If one could actually enter the cell, the protoplasm would no longer look like a grayish granular material as it did from the first perspective. Descending into the world of molecules, one would find a bewildering array of shapes and sizes. Forming a more or less uniform basis for the whole mass are the familiar water molecules. These dart hither and thither with no apparent driving force behind them, in the movement called heat. They strike each other and rebound. Periodically they may strike some of the larger, more complex molecules that move ponderously among them, and not infrequently they stick to these. At times, when this happens, the larger molecule breaks apart, and each part goes its sep-

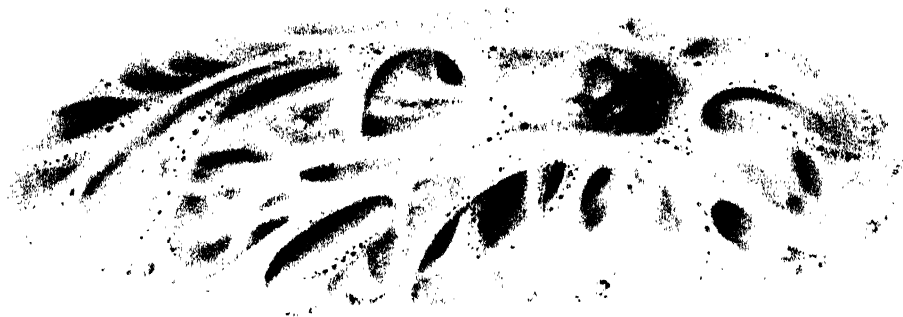


Fig. 34. An artist's conception of the organization which probably exists in protoplasm, the complex chemical and physical structure of which living things are composed.

arate way with accelerated speed. Many of the larger molecules in the cell — and this should be noted particularly — are attached to others like them and thus form great porous sheets or networks like coarse sponges. These are membranes, and are extremely important to the behavior of the cell.

Between the pores of these three-dimensional chains, smaller molecules dart in and out, and larger ones try the passage but are barred by their size and bounce back as though they had hit a solid wall. We are witnessing *osmosis*, a diffusion phenomenon that will merit close study later. Some molecules that look small enough to pass through the pores nevertheless appear to be repelled by an invisible force when they approach the screen of the chain-molecules. Others appear to be attracted by it and may even stick to it. If this happens, the whole network of molecules may suddenly disintegrate and the parts wander off in various directions. The molecular nets are the membranes of porous but solid structures called *gels*, and we have witnessed the disintegration of some of them into more liquid structures or *sols*.¹ Here and there, floating in the constellations of smaller molecules, are globular island universes composed of masses of larger molecules surrounded by sheets composed of still others that appear to be holding them together as a toy balloon may hold

water. These spherical masses of large, sluggishly moving molecules glisten and shine at a distance. They are droplets of oils and fats, held together or stabilized by layers of certain surface-active molecules.

Protoplasm as a Mechanism

This will do for a first brief look into the world of protoplasm. New terms and form-patterns have appeared, and most of these will require further explanation. Noteworthy in the scene was its ceaseless activity, movement, and change. Also noteworthy is the fact that these molecules differ only in size and complexity from those in the world of non-living molecules. Those within the protoplasm move about and change in structure, but they do nothing that is not in the nature of all molecules. None of them can be called alive. They do not differ in their behavior from the obviously inanimate molecules of water that form the main bulk of the protoplasm. The sum total of all this activity is life, but no one part of it can rightfully be so called. The essence of life is in the whole of it — as motion in an engine inheres not in the separate parts but in the motor as a whole.

Chemical Constituents of Protoplasm

Elements. The principal elements which compose protoplasm are common and relatively few in number. Four are primary. Carbon (C),

¹ See pages 50-51 and pages 56-57.

hydrogen (H), oxygen (O), and nitrogen (N) form the bulk of all the compounds of protoplasm. Carbon is the core of all these compounds, as water is the medium in which all life activities occur. As we have seen (page 37), the structure of carbon and its unique ability to combine with itself to form long chains and rings makes it capable of forming many different compounds, and this accounts for its importance in protoplasm. In lesser quantity, but also essential, are the elements phosphorus (P), potassium (K), iodine (I), sulfur (S), calcium (Ca), iron (Fe), magnesium (Mg), sodium (Na), and chlorine (Cl). Still others such as boron (B), copper (Cu), cobalt (Co), zinc (Zn), Manganese (Mn), and others are essential as trace elements in some organisms. This may seem a formidable list, but the important elements represent only a fraction of the existing number, and only a few form the bulk of all protoplasmic compounds.

Compounds. All of these elements form compounds, few of which are found today anywhere in nature except as a product of the activities of living organisms. Protoplasmic compounds may therefore be classified into two main groups: inorganic and organic. *Inorganic compounds* are those commonly found in nature, with or without the aid of living organisms. Many of these are nevertheless essential in the composition of protoplasm. The inorganic components of protoplasm are primarily water, inorganic salts, and various dissolved gases such as nitrogen, oxygen, and carbon dioxide. The *organic compounds* may be classified in three great groups, carbohydrates, fatty substances or lipoids, and proteins. Organic compounds usually play a dual role in protoplasm. They are carriers of energy and may decompose to yield it; and they serve as the structural units of which the protoplasm is composed.

Inorganic Compounds

The Importance of Water. Not only is water the most abundant ingredient of protoplasm, but it also has many other properties that eminently fit it as the carrier of life. It dis-

solves a greater variety of substances than any other liquid; it is unequalled in enhancing the chemical activity of these solutes; it dissociates itself into the highly active OH^- and H^+ ions sufficiently for chemical activity. Thus water plays an active part in many chemical changes. It also has a high heat capacity, relatively low viscosity, and high surface tension. Thus water is the main vehicle of the substances that produce life. Scattered throughout this watery medium in protoplasm are many other substances that considerably alter its fluid nature. The ions formed from inorganic salts, acids, and bases modify the nature of the solution. Organic compounds may so decrease its fluidity as to render it a solid or semi-solid. The protoplasmic streaming in the *Eloëa* leaf, the membranes, the diffusion of molecules through them, and the changes from sol to gel and back again — these are the actions of other substances in a watery medium — the activities of life. Let us see more closely how these things take place.

Kinds of Organic Compounds

Carbohydrates. These are the principal energy-giving compounds found in protoplasm, although in the cell walls of plants, which are composed of the carbohydrate cellulose, they play an important structural role. Glucose, one of the simplest carbohydrates, is most important as a source of energy. It is produced by green plants (see page 65) and is a basic organic compound. Carbohydrates are compounds consisting only of carbon, oxygen, and hydrogen in the proportion of CH_2O . Most carbohydrates are based upon chains of six carbon atoms, or upon groups of such chains. Thus glucose is represented by the formula $\text{C}_6\text{H}_{12}\text{O}_6$.

Fats. The fats and fat-like substances are “greasy” and relatively insoluble in water. They include fats which are liquid at room temperature and are called oils. Fats, like carbohydrates, are important fuel or energy compounds, but they also serve vital structural purposes, not only in the complex anatomy of a multicellular organism, but as a structural

part of protoplasm itself. Besides the true fats, represented by such substances as lard, butter-fat, corn-oil, and others, there are complex fatty substances, phospholipins and sterols, important in the structure and functioning of protoplasm. True fats are composed of carbon, hydrogen, and oxygen, the last only in small quantities. Carbon and hydrogen are present in a ratio of two hydrogen atoms to one carbon.

Proteins. These are of primary importance in the structure and functioning of protoplasm. Indeed, certain proteins may be considered almost the essence of protoplasm, although their activities are possible only within the entire complex. The basis for such a sweeping statement becomes apparent when we learn that cell membranes, the protoplasmic catalysts called enzymes (see page 62), and the genes — the all-important determiners of hereditary characteristics — are mainly of protein composition. Proteins are the most complex of all compounds and may consist of thousands of atoms per molecule. As in other compounds, carbon, oxygen, and hydrogen form the bulk of the protein structure, but a fourth essential element, nitrogen, is always present, and two others, sulfur and phosphorus, are frequent. Other elements may also form part of the structure of protein molecules.

Of all the proteins, the *nucleoproteins* must be considered of first importance, for these characterize the chromosomes, structures of fundamental importance in the reproduction of cells. The genes which compose the chromosomes may be individual nucleoprotein molecules. Through their specific catalytic action the genes direct and control, individually and collectively, the total activities and the character of the cell. The nucleoprotein molecules are formed of a simple protein base (protamine, histone, etc.), nucleic acid, and certain carbohydrates. The number of possible nucleoprotein combinations is almost unlimited, and thus each gene may be pictured as a unique molecule capable of autosynthesis and operating in the cell together with other substances to direct certain chemical reactions through which protoplasm appears to function.

ORGANIZATION AND BEHAVIOR OF PROTOPLASM

All these chemical components of protoplasm are in a constantly changing but highly organized state possessing both fluidity and solidity. Hence protoplasm is mobile and dynamic and yet stable enough so that chemical reactions can be guided along specific paths to specific ends.

The Consistency of Protoplasm

In a gas, the molecules fly past each other with slight interference; in a liquid, where they are much closer, the molecules exert cohesive forces on each other, and so form a mass of definite volume and shape; in a solid, the cohesive forces hold them together and greatly restrict their mobility. None of these states would permit the combination of internal mobility, order, and stability found in protoplasm. Some intermediate or mixed condition must prevail.

Erwin Schrödinger, physicist and Nobel Prize winner, has suggested that there is a considerable correspondence in structure between a molecule, a true solid, and a crystal; for the stability of a true solid, some say, is achieved only when the forces that hold the atoms in place in a molecule also hold the molecules together in a specific pattern, as in a crystal. A crystal would thus be considered as in fact one huge molecule. Any form of solid not crystalline — the so-called amorphous solids, such as glass and plastics — would then really be liquids with a very high degree of viscosity. Although protoplasm itself is a liquid system, it contains parts which have a semi-crystalline structure. Protoplasm thus possesses both the essential characteristics of a liquid and the virtues of stability ordinarily found only in a true solid. It consists of a ground substance of water through which are dispersed various chemical compounds in the form of single molecules or groups of molecules.

Dispersions

In protoplasm, water is the medium in which the various substances are dispersed as par-

ticles. Such particles can be roughly classified according to size, or as to whether they are composed of single molecules or of groups of molecules, and this difference has a pronounced effect on the appearance and behavior of a dispersion. If the particles are single molecules, as in sugar water, the system is called a *solution*, whereas if each particle is made up of several molecules, as in muddy water, the system is a *suspension*. If the solution consists of small molecules (10^{-6} mm. in diameter), it is a true *crystalloidal* solution. If the molecules are larger than this, but not large enough to be seen microscopically (10^{-4} mm.), the solution is said to be *colloidal*. And particles that consist of groups of smaller molecules form *colloidal suspensions*. Protoplasm is both a true solution of solutes in water and also a colloidal emulsion.

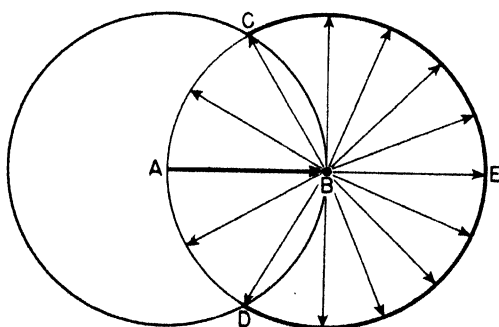
The nature of an emulsion may be better understood if we consider first a familiar phenomenon. When an oil is shaken up with water it forms a temporary, unstable emulsion. Because water has greater polarity than oil, and consequently greater cohesion, water tends to cling to water more tenaciously than oil to oil. Hence when oil and water are shaken up together, so that both are broken up, the water particles immediately reunite to form a *continuous phase*, while the oil remains suspended in droplets, the *dispersed phase*. This emulsion persists only for a short time because the oil, being lighter than water, rises to the top where the oil droplets can *coalesce* again. Such an emulsion can be stabilized by adding to it a substance that is both polar and non-polar, such as soap. Any such particle will mingle at its polar end with water, which is polar, and at its non-polar end with oil, which is non-polar. As a result the oil droplets will be completely covered by a film of the soap, which prevents them from coalescing.

In protoplasm the continuous phase is usually the watery solution and the separate particles or droplets of fatty and protein nature make up the dispersed phase. The colloidal system is stabilized by the presence within it of various polar non-polar substances. In this

state the protoplasm will flow readily. When, as may often happen, the particles adhere to one another to form a three-dimensional lattice-work extending throughout the medium, then the protoplasm becomes highly viscous or relatively solid. Like familiar jellies, which are reversible between these two states, protoplasm is capable of changing from thick to thin, solid to fluid, and back again.

Some constituents of protoplasm, such as sugar, glycerol, and fats, do not tend to dissociate into ions. Other molecules, such as amino acids and proteins, dissociate into ions only slightly, being weakly polar. Still others, like salts, acids, and bases, both organic and inorganic, dissociate freely. Substances that ionize readily diffuse as ions, generally at rates greater than that of the undissociated bigger molecules from which they come. Also, electrical charges will speed up ions of opposite charge and slow down ions of a similar charge. Non-polar molecules dissolve best in non-polar solvents, such as oils, and polar molecules dissolve best in polar solvents, like water. This too has great application in the behavior of substances in protoplasm, for the distribution of substances will depend upon their solubility either in the continuous phase of the colloidal system or in the dispersed phase, and upon their ability to penetrate membranes, which are generally highly fatty and bear electrical charges. Amino acids and proteins can act both as acids and bases; that is, they are *amphoteric*. That is, a protein will react as a base with any acid entering the protoplasm and as

Fig. 35. Diffusion occurs because more paths lead away from than back towards a previous position.



an acid with any base. Because of this strong reactivity and because any radical shift from neutrality toward acidity or alkalinity destroys the properties of the proteins in the protoplasm, these must be shielded or buffered against the action of strong acids and bases. Very important in the blood of animals, for example, are various inorganic salts such as carbonates and phosphates, which act as buffers by combining with strong acids and bases and replacing them by weak acids and bases. The proteins in the fluid part of the blood also act as buffers to protect the proteins within the protoplasm from exposure to strong acids and bases. Hemoglobin, the red protein inside red blood cells, acts in an analogous way. From these facts it is clear that the pH , a measure of the concentration of H^+ and OH^- ions present in the system, is a factor of inescapable significance to the behavior of protoplasm.

Diffusion

All molecules, ions, and other sorts of particles, because of their heat energy, are in constant motion and may move with equal probability in any direction. Since more paths lead away from a previous location than back toward it, the sum of successive movements results in a particle moving farther and farther from its original position (Fig. 35). This tendency to scatter in a random fashion is influenced by the degree of attraction between them, depending in turn on their structure, electrical charge or lack of it, cohesion, adhesion, and so on. Molecules of course scatter most rapidly and freely in a gas and least freely in a solid. This scattering is *diffusion*. We all know how, when a bottle of perfume is opened, a person at the opposite end of the room is soon able to smell it. Molecules of the odorous substance have actually crossed the room. In solution, diffusion is slower but more readily visible. Drop a crystal of a colored soluble substance into a beaker of water and allow the beaker to stand perfectly still and covered. Even against the action of gravity, the molecules of the solute will slowly diffuse through the solvent, until they are equally dis-

tributed everywhere. This illustrates one of the principal laws of diffusion, that substances diffuse from points where they are more concentrated to all regions where they are less concentrated. A second important principle will become clear if the rates of diffusion of particles of two different sizes are compared in the same solution. The tiny molecules of a colored salt will diffuse far more rapidly than the relatively enormous particles of a dye, which are of colloid dimensions. Thus in protoplasm, where both molecules and ions of small size are present as well as colloid particles of large size, the rates of diffusion must be considered separately for different substances.

Surfaces and Membranes

Because of its structure, protoplasm is full of surfaces. It is hard to believe, although quite true, that the total amount of surface in the protoplasm of an *Elodea* cell, which can be seen only under the microscope, is nevertheless sufficient if spread out to cover a couple of the walls of a good sized room. This is because the subdivision of matter into smaller and smaller particles increases the ratio of surface to volume (see page 24). This has a number of very important consequences affecting the behavior of protoplasm. In the first place, particular substances become adsorbed upon certain surfaces, in accordance with their chemical nature. This was clear in the previous example of the adsorption of soap upon the surface between water and oil. (The adsorption of substances may have important direct effects, as in stabilizing a colloidal system, but the matter goes farther.) Different substances adsorbed upon the same surface are brought into much more intimate contact than when they were freely diffusing through the solution, and if capable of chemical reaction, will react with one another at a vastly increased rate. These phenomena lead to the production of different sorts of membranes surrounding the dispersed phases of the protoplasmic emulsion. Substances also have different solubility in different phases and pass through different membranes with varying degrees of ease. Polar

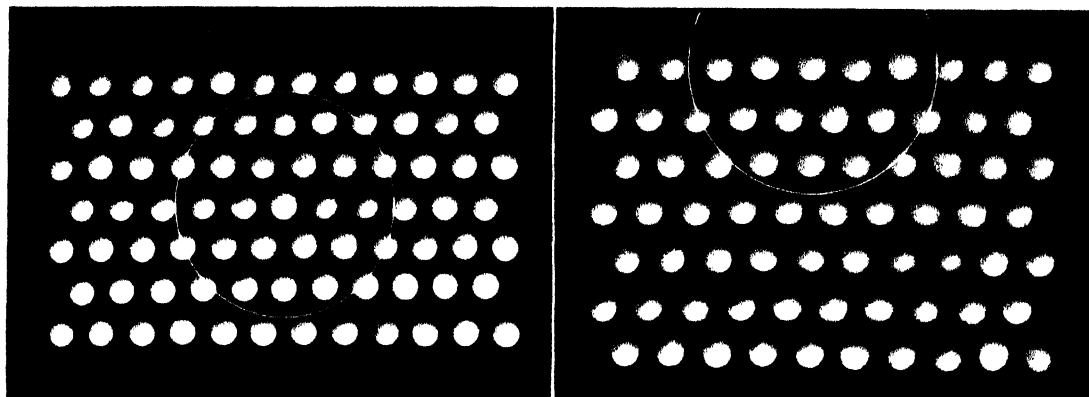


Fig. 36. Stress and balance within a group of molecules. Those at the center of the circle are attracted equally in all directions and will not tend to wander in any particular direction. But molecules on the surface of the group (at right) are attracted only from below and from the sides and tend to be drawn downward.

substances which dissolve in water may pass freely through the continuous phase. But non-polar substances, dissolved in the dispersed phases, will be virtually unable to pass from one point to another because there is no continuous bridge for them. They are isolated in the droplets. Consequently the separate microscopic bodies and droplets and phases of the protoplasm become so many separate sorts of chemical factories, in which processes can go on in regular and orderly routine without getting mixed up with other sorts of chemical reactions necessary in the complex processes of life.

The molecules at such surfaces are under different attractive forces than those in the interior of a phase, either dispersed or continuous. This distribution of forces (Fig. 36) produces what in essence is an elastic membrane over the surface, marked by surface tension (see page 23). Surface tension is of the utmost importance to the behavior of protoplasm, accounting for properties of the surface membrane on the outside of each cell as well as of those surrounding separate structures and phases within it. Any solute that lowers surface tension tends to accumulate in the surface membrane. This reduces the potential energy of the membrane and kinetic energy in some form or other is released. This may be heat or motion.

An Experiment with Camphor. A simple experiment will show how a change in surface

tension will liberate potential energy. Fill a dish with water and scrape some small camphor chips onto its surface, and the chips whirl and dart about on the surface as though alive and they will do so until the camphor evaporates (Fig. 37). The explanation is simple. Camphor is non-polar and both soluble and volatile. Its molecules temporarily displace some of the water molecules at the surface of the water and thus break the surface tension at that point. The water film reacts to such a break just as any elastic film would

Fig. 37. Trails left by camphor particles moving on the surface of water.



react: it snaps back in all directions away from the point of the break. If the camphor particle were entirely symmetrical and gave off exactly the same amount of camphor in all directions, the particle would probably sit perfectly still while the surface film of the water around it became replaced with camphor molecules. But since no such particle is ever quite symmetrical, the side with the greatest surface gives off most camphor, and as this causes the greater break in the surface membrane of the water, the camphor particle is dragged in the opposite direction by the less rapidly receding film of water.

The erratic dance of the camphor may be brought to a dramatic end by touching the surface of the water with a pencil point which has just been rubbed on a cake of soap. Since soap is polar-non-polar it accumulates on the surface of the water and greatly lowers its surface tension. The camphor particles will be crowded toward the edge of the dish and all action will cease. The surface of the water will then no longer consist of water but of soap particles, which have a much lower surface tension. Similar effects — though vastly more complex than this — are constantly occurring in protoplasm as the surface tension changes at the membrane between two substances within a cell or in the outer cell membrane itself.

Membranes and Permeability

The accumulation of substances that lower surface tension in the cell membrane also affects the entrance to or exclusion from cells of solutes, that is, the permeability of the cell membrane. Fatty substances, like soaps, are especially concentrated in cell membranes, and consequently substances that will dissolve in fats are able to enter cells with great rapidity. Thus the nature of the *permeability* of cell membranes depends upon the existence of surface tension, among other things.

In addition to the lipid constituents, the cell membrane has protein components and perhaps also pores. The membrane is therefore a mosaic which differs in its permeability from

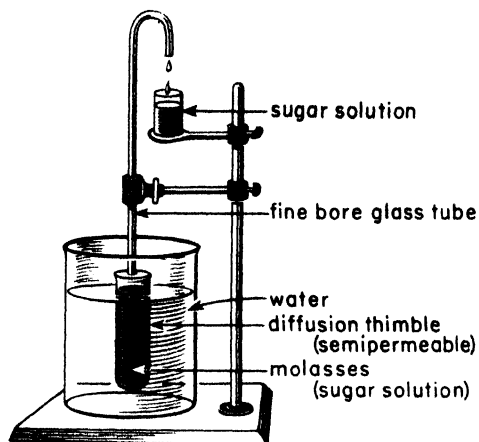


Fig. 38. Demonstration of osmosis.

region to region. Because the membrane also bears a charge, the type of ions which can penetrate it varies with the nature of the charge. If the charge is positive, as in a normal red blood cell, for example, negative ions can enter and leave the cell freely, but positive ions are repelled and cannot get through so easily. The charge on the membrane varies from positive to negative with the prevalent external acidity or alkalinity, so that the *pH* of the medium also influences permeability to a marked extent.

Osmosis

Diffusion occurs not only within protoplasm but also through the outer cell membrane, subject to the factors which modify permeability, outlined above. When a membrane is differentially permeable to various substances, a special phenomenon called *osmosis* occurs. A simple demonstration, using a much less complex system than protoplasm, will help to explain this.

The device illustrated in (Fig. 38) consists of a thimble-shaped parchment filled with molasses (sugar consisting of relatively large molecules dissolved in water molecules). A rubber stopper pierced by a thin glass tube closes the top of the thimble, which is placed in a beaker full of water and held with a clamp. If the glass tube is fine enough

in caliber, the molasses solution in the thimble will begin to rise in the tube in a matter of minutes, and in an hour or two will climb the several feet to the top of the tube and overflow.

This happens because the volume of liquid in the thimble has increased. If we measure the level of the water in the beaker, we can also observe that it has gone down slightly. For water from the beaker has gone through the membrane into the molasses solution within. But why should the water molecules go in and apparently not out? Actually they go both in and out, though more of them enter the thimble than leave it. The real question, then, is this: Why is the passage of water not equal in both directions? And the answer is that the membrane is *semi-permeable*. In other words, the smaller water molecules can pass through it, but the larger sugar molecules cannot (Fig. 39). Just as many molecules strike a given area of the membrane on the outer side as on the inner. But inside the thimble are many sugar molecules which cannot penetrate, while outside are only water molecules which can. Therefore, since more water molecules strike the outer than the inner surface, more of them will slip through. Since more water molecules flow in through the membrane than out, the solution will increase in volume and will climb in the tube until an equilibrium has again been established and just as many water molecules flow out as in. That condition will occur only when the sugar concentration in the tube has been reduced to the vanishing point, or when the increased inflow has raised the pressure within the membrane until the molecules are packed so tightly that just as many water molecules hit a given surface on the inside as on the outside. This is no contravention of the laws of diffusion, as it seems at first glance. The sugar is unable to diffuse through the membrane because its molecules are too large for the pores. The water, which is able to pass through the membrane, is moving from a region where it is more highly concentrated (pure water) to one in which it is less concentrated because it is mixed with sugar molecules. Osmosis is thus a movement of the solvent — in living systems

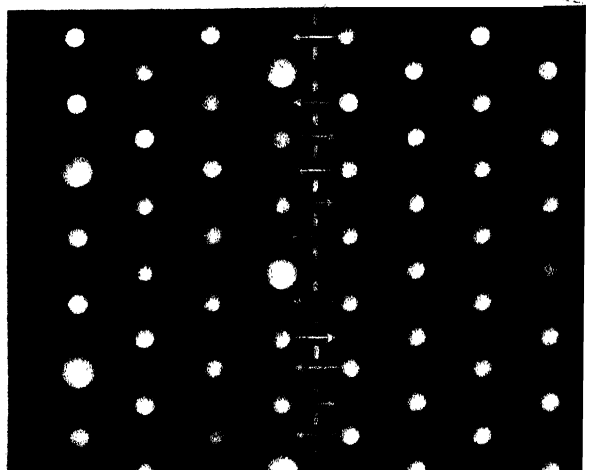
virtually always water — through the differentially permeable membrane. The osmotic pressure of a solution is the pressure of the water diffusing into it, and is measured by the concentration of non-permeable solutes in the solution,¹ in comparison with pure water. Osmotic pressure is of very great importance in living cells, being responsible for the flow of water in or out of the cells and the turgor of plant cells which gives them rigidity.

Osmosis in Living Tissue

With some understanding of osmosis and osmotic pressure, it is possible to understand certain phenomena in the behavior of plant and animal cells. To take a simple instance, we can now see why a lettuce leaf placed in a concentrated salt solution becomes soft and limp. Salt does not pass through the cell membranes of the leaf as readily as water, and the osmotic pressure of the salt solution is greater than that of the protoplasm. Hence more water will leave the cell than will enter it, and the cell goes limp. Place the wilted leaf in fresh water and in a short time it will be crisp again, because the pure water on the outside

¹ Actually, solutes which can pass through the membrane but do so more slowly than water will also add to the osmotic pressure of the cell, temporarily.

Fig. 39. Diagram illustrating the theory of osmosis. The dotted line represents a semi-permeable membrane. To the left is a sugar solution. The small water molecules can pass through the membrane; sugar molecules are too large to pass. To the right are water molecules only; hence more water molecules will pass from right to left than in the opposite direction.



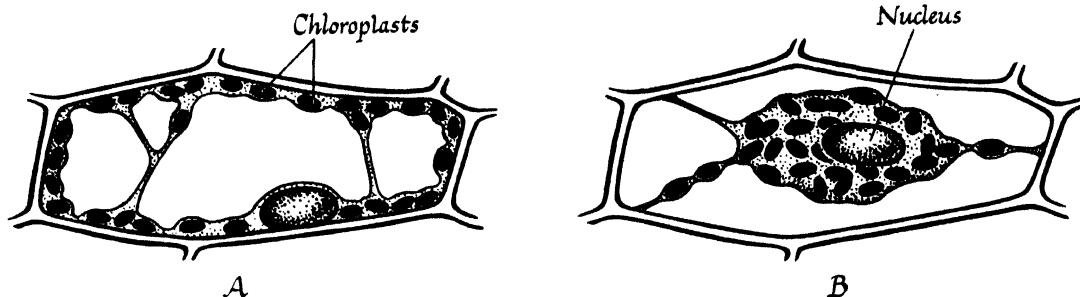


Fig. 40. *A.* Single cell of *Elodea* as it would appear under high magnification. *B.* Plasmolysis in the cell of *Elodea*.

has no osmotic pressure, whereas the protoplasm has, and water molecules therefore pass into the cells. Placing the lettuce leaf in plain boiling water will also produce limpness, but in this case crispness cannot be restored, for the boiling water destroys the living semi-permeable membrane so that the wall of the cell is afterwards freely permeable to most molecules and no osmosis will occur.

The phenomenon of wilting may be more effectively observed under a microscope. The cobblestone cells of the *Elodea* leaf are then clearly visible, and the osmotic pressure within the cells is balanced by the resistance of the cell walls. But if a salt solution is added, almost at once the layer of protoplasm shrinks away from the outer cell wall, until only a ball of protoplasm containing the clump of chloroplasts lies in the middle of the cell with water all around (Fig. 40). This action, called *plasmolysis*, shows that the protoplasm is actually encased by two coverings, the outer wall, which is dead and inert, and which is freely permeable, as the immediate penetration of the salt solution shows; and the inner membrane, which is a part of the living protoplasm and is only semi-permeable, since it allows the water molecules to pass outward but does not allow the salt to pass inward to any great extent.

A red blood cell seen under the microscope reacts similarly. Add water to the slide and many of the cells swell into balloon-like structures and may even burst. Add a moderately strong salt solution and they shrink and crumple to stylized stars. From this it may

be concluded that blood cells normally have a higher osmotic pressure than plain water but less than the salt solution. The blood plasma, of course, has just the same osmotic pressure as the blood cells, that is, they are *isotonic*. A salt solution could of course be made up that had just the same osmotic pressure as the blood plasma. This would keep the blood cells in their normal condition. One with a higher osmotic pressure is said to be *hypertonic*; and one with a lower is called *hypotonic*. Osmosis maintains the normal shape of the body cells and controls the entrance and exit of water from the cell.

Phase Reversal

If the relationship between the two phases of a colloidal emulsion is changed, the whole nature of the emulsion is transformed. Such a change is termed a *phase reversal*. This too happens in protoplasm, and when it does, the nature of the substance which can diffuse of course changes also. Not only is the permeability of such an emulsion changed, but its fluidity or viscosity is also changed. Such is the manner in which protoplasm adjusts itself to its changing environment. Its permeability changes to meet its momentary needs, as does its consistency.

Effect of the Stabilizer. All that is necessary to produce a phase reversal (Fig. 41) is to change the chemical composition of the stabilizer. For example, let us return to the sample system of oil and water, stabilized by soap. Soap can be any of a number of different compounds produced by treating a fatty acid in

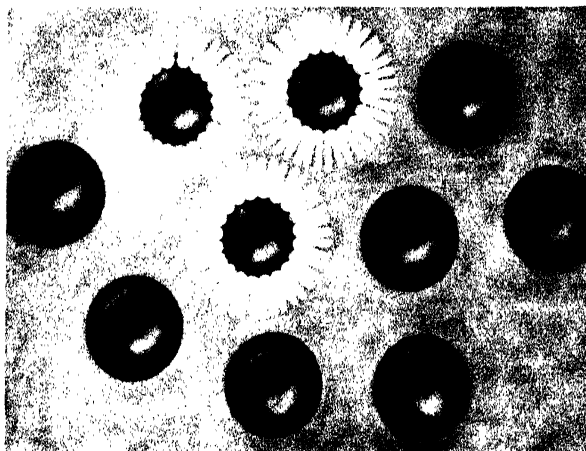
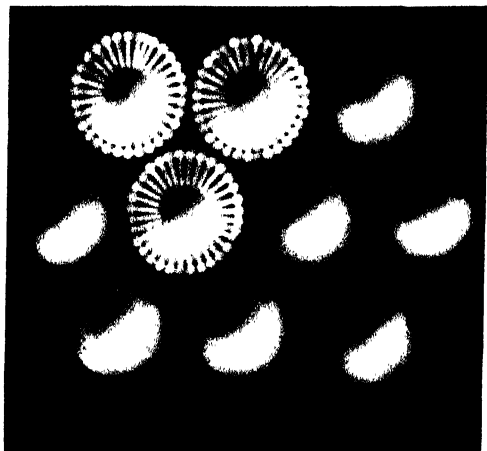
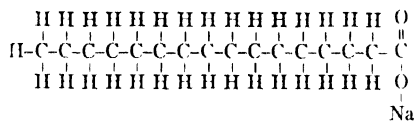


Fig. 41. A stabilized emulsion. At left, soap molecules are club-shaped. The “handle” is non-polar and dissolves in oil. The “head” is polar and dissolves in water. Changing the stabilizer (right) reverses the phases.

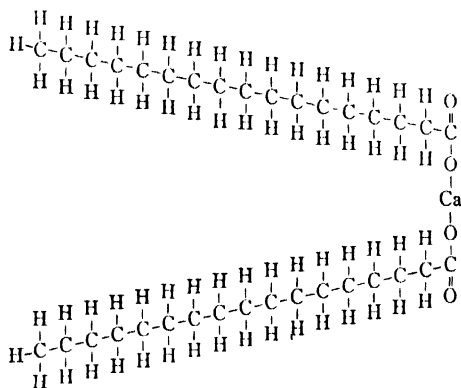
which the ionizable hydrogen has been replaced by a metallic ion such as sodium (Na^+), like this:



By interaction with the water, the polar end of this ordinary soap molecule — the end that carries the Na — will in effect be bulkier than the non-polar chain of carbon and hydrogen. Therefore, if many such conical molecules are packed side by side in a single layer, the result will not be a flat sheet, but a curved surface. Since the wider part of the cone is the polar end, that part will form the outer surface of the curved sheet, while the non-polar portion will form the inner surface. If this sheet of soap is pictured as forming at the interfacial surface between water and oil, it is clear that the non-polar oil will be on the inner side of the curved soap film while the water will be on the polar outside. Such an arrangement would naturally result in oil droplets surrounded by water.

Changing the Stabilizer. By adding a salt rich in some other metallic ion, for instance CaCl_2 , many of the Na ions will be replaced by Ca. Since the Ca ion is bivalent this changes

the whole structure of the soap molecule, so that instead of a single chain of carbons and hydrogen, two divergent chains attach themselves to each Ca ion.



Thus in the calcium soap the non-polar end is the wider side of the cone. Such a soap would produce a film curved exactly opposite to that of the Na soap. Thus the Ca soap will support an emulsion of water droplets surrounded by oil.

The Reversal. Such conditions can readily be observed under a microscope. A drop of soap-stabilized emulsion — in which oil has been stained red for better visibility — will show a beautiful pattern of countless red spheres surrounded by clear water. If a drop

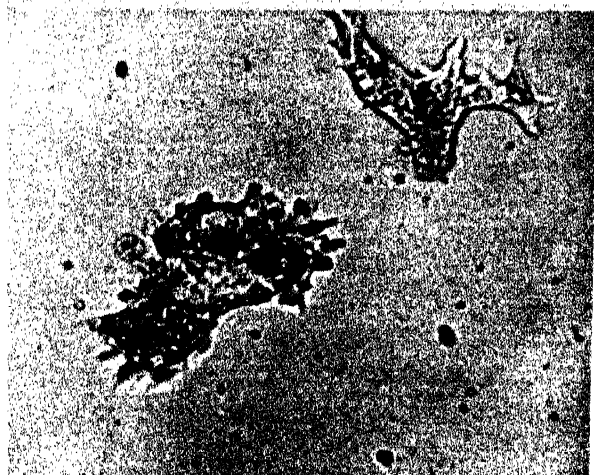


Fig. 42. Living amoebas, as seen under the microscope.

of CaCl_2 is added, action begins at once. As the CaCl_2 spreads, the oil droplets momentarily lose their protective coat of Na soap, and wherever such droplets touch each other, they coalesce with startling suddenness. This action progresses as the invisible CaCl_2 flows across the field of vision. But the water does not at once form into droplets, and will not, until the now oily and sticky mass is stirred so as once more to break up both phases into droplets. This allows both oil and water droplets to arrange themselves in conformity with the forces of the new soap molecules acting upon them. In the re-stirred emulsion, droplets of clear water are surrounded by a transparent sheet of red-stained oil. Phase reversal has been achieved.

These phenomena have been described at such length because they appear to play a leading role in the highly sensitive adjustment of protoplasm to changing environmental influences. Without an understanding of these processes, the behavior of protoplasm as displayed, for example, by a living amoeba, remains an incomprehensible mystery. But with this knowledge, we may at least gain some inkling of the mechanism by which solutes diffuse from one region of a cell to another and of how the cell responds to its environment by moving. The responses of a cell to environmental demands become chemical responses controlled by the activities of

enzymes, which in turn exert their influence on the balance of emulsoid stabilizers and thus on the emulsoid state, in this manner determining rate and direction of diffusion and consequent further chemical reactions.

ANOTHER VIEW OF PROTOPLASM

Chemical Reactions and Protoplasm

With this insight into some of the physico-chemical phenomena exhibited by masses of molecules under varying conditions, we may now take another look at an actual bit of protoplasm, this time not a piece of plant tissue but a single cell which is also a free-living animal cell, an amoeba.

Under the microscope, a living amoeba appears to be simply an animated mass of varied granules floating in a fluid (Fig. 42). Most of its enormous complexity and intricate organization are quite invisible. Dissolved or suspended within the watery medium are minute particles — many of them colloidal — of various substances, including the organic carbohydrates, fats, and proteins. Polar and non-polar substances may form emulsions, and protein ions may form intricate chains and networks of molecules — membranes — at the points where different substances meet. Often these appear to be most delicately balanced, so that emulsions change in phase, membranes dissolve and new ones appear, and substances diffuse throughout the protoplasm or are arrested by the barriers of the membranes. Within the confines of the cell, the protoplasm appears to be generally in motion, and the movement of the amoeba from place to place grows out of this.

Motion in the Living Amoeba. The amoeba is generally pushing out a protrusion of its substance, called a pseudopod or "false foot," in one direction or another, and then flowing along after it until the pseudopod is re-absorbed. In an amoeba, the granular part of the protoplasm appears to be surrounded by a clear area, and outside of this is a limiting protoplasmic membrane, which also is a part of the living substance and is constantly undergoing chemical change like the

rest. Here, there, or anywhere, the membrane may suddenly bulge outward, and as it does so, the liquid content of the cell flows into the protrusion. The observer gets the impression that this occurs because the membrane weakens, and this appears possible, because of a change in surface tension augmented by internal pressure.

How could such a change in surface tension come about? In the mercury amoeba (page 43) it is clear how this takes place. The potassium dichromate dissolves and reacts with the mercury, oxidizing some of the molecules of mercury on the surface. These turn brown. The oxidized molecules have lower cohesion than the unaltered mercury so that they are pushed apart and out by the pressure of the mercury molecules within. When these reach the surface, they are in turn oxidized and the process is repeated. Thus changes in surface tension release kinetic energy in the form of motion. The movement in the living amoeba is perhaps fundamentally similar to that which operates in the mercury amoeba. Lowered surface tension and internal pressure against the weakened portion of the membrane result in the formation of these pseudopods. The question is, then, what induces these physical changes. Perhaps they come about through the myriad chemical influences which impinge upon the amoeba from its environment, and modify the delicately balanced state of the colloidal phases in the cell membrane.

Because the protoplasm of the amoeba has far greater osmotic pressure than the fresh water in which it lives, water constantly enters the amoeba and tends to dilute its protoplasm beyond the point where it can retain its organization and continue to function in a living fashion. Hence the amoeba, like other similar fresh water animalcules, must have a means of eliminating the excess water which enters and dilutes it. Such a structure, a sort of miniature hydraulic pump, it has, and the operation of this will be described more fully in Chapter 13.

To sum up: the essential structure of protoplasm is intermediate between liquid and solid, so that it has the fluidity of the former and the

stability of the latter. Its ceaseless dynamic motion results from immensely complex chemical change. Important to its behavior are ionization, diffusion, osmosis, the formation of surfaces and membranes in emulsions and the phase reversal of the latter, the surface tension and the kinetic energy of motion. This is not the entire nature of protoplasm, but these chemical and physical processes shed considerable light on the basic character of many life activities.

The Physico-Chemical Hypothesis

On the strength of increasing knowledge of chemical and physical processes in non-protoplasmic as well as in protoplasmic systems, where parallels are increasingly revealed, it may be postulated that if knowledge were still greater, the behavior of protoplasm might be interpreted wholly in such terms. The behavior of a living amoeba, like that of a mercury amoeba, might be explained in terms of physical and chemical changes which obey the same laws as those governing such changes in inanimate nature. Knowing that the mercury is inanimate, one is not tempted to explain its motion in terms of desire, hunger, purpose, or will. So similar is the appearance of this behavior to that of the living organism that one may be led to question the value of such terms as really explaining the behavior of life. The concepts are perhaps mere semantic disguises for our ignorance of what actually occurs.

The behavior of an amoeba might then be explained as follows: a particle of food suffers partial solution in water. Some of the dissolved molecules and ions diffuse toward the membrane of the amoeba, and in conjunction with other molecules that strike the membrane from inside the cell, cause changes such as those previously described. The membrane bulges, the pseudopod reaches forward, and eventually the amoeba may flow completely around the food particle and ingest it. In familiar terminology, the amoeba senses food, discovers that it is hungry, wills to form a pseudopod at the right point, and cunningly

surrounds the food particle. In this newer terminology, which attempts to avoid implying what cannot be demonstrated, the food particles diffuse toward the membrane of the amoeba, there causing chemical and physical changes which so weaken the labile structure that internal osmotic pressure causes a flow of protoplasm into the weakened area, thus protruding a pseudopod and a general flow toward the exciting particle. Desire and purpose are interpreted as physico-chemical changes. Hunger may have been involved, but it becomes transformed from a sensation into a physico-chemical state of the protoplasm and its surrounding membrane.

It may then be asked what this has done to the "personality" of the amoeba. Has the creature been deprived of its individuality by this attack on the secrets of its structure and behavior? Life is still exactly what it was before; we have merely made a beginning toward analyzing it. It may be argued — and sometimes is — that this explanation is very far from complete and hence very crude, and that therefore special laws must after all be held accountable. But such an argument would hardly be more valid than that of the native who, baffled by the intricacies of an airplane, simply throws up his hands and says it flies because it is endowed with the spirit of flight.

To return to the amoeba, one may ask why all this fuss about it. After all, the amoeba is a small part of the panorama of life, and what applies to the amoeba does not necessarily apply to other creatures, and especially to man. Yet, if the science of biology teaches nothing else, it does teach the fact of the universal likeness of protoplasm, be it that of an amoeba, an oak tree, or a human being. Basically they are alike, differing only in the details of the performance of their functions. The fact that man is infinitely more complex than the amoeba applies to the aggregate of cells of which he is composed rather than to the individual cells of his body. The white blood cells of the

human body appear to occupy no higher plane of organization than does the amoeba in the pond. Indeed, many single-celled animals have attained levels of complexity hardly attained by a human cell, though the complexity of interaction between the billions of cells in the human body is such as to exceed comprehension.

Yet, though by no means established, it is upon the physico-chemical hypothesis that the modern biologist builds his researches and has made what progress he has made. It is the assumption that the unknown is explainable in terms of the known that gives the man of research the courage for further attempts to pry into the unknown, whereas an unnecessary assumption of special or mystical properties, unsusceptible of scientific study, effectively discourages scientific effort. After seriously and conscientiously surveying the fields and methods of science, each individual must eventually formulate his own opinions, though they remain only opinions. But opinion formed without a conscientious survey of facts already known is mere prejudice, and there is no room for this in science.

Can Life Be Defined?

And now, our preliminary survey done, we are faced again by our initial question: What is life? Perhaps we can do no better than to say: Life is heat, change, and motion — the ceaseless dartings to and fro, chemical marriages and divorces, entrances and exits of the molecules and ions in the watery gel we call protoplasm. Life is order and organization, complexity piled on complexity, intricacy woven into intricacy, until one can understand the nature of the system only by crude abstractions. Life is no one thing but many things, physico-chemical yet aspiring to a higher level of responsiveness, of adaptive and appropriate answers to the problems of existence. Life is continuity of pattern in the midst of flux. Life is a magnificent drama of evolution.

Metabolism and Nutrition

Protoplasm, then, is a staggeringly complex chemical system in a ceaseless round of change. Since change means motion and motion takes energy, protoplasm is constantly consuming itself, burning itself up, in order to stay alive. At the same time, it is also taking in new substance — new fuel to burn and new material to replace its worn out parts or to build new ones. These activities of building and destroying, storing and consuming, are in a sense the very essence of life and may be summed up in the word *metabolism* (Gr. *metabolē* = change). Every living cell is constantly engaged in metabolism, and every organism. Many organisms in curious ways assist and complement each other in the ceaseless struggle for rare or essential substances, so that the whole world of life on earth is one highly integrated metabolic system. In photosynthesis plants take in carbon dioxide and give off oxygen as a waste, while animals do just the opposite. Animals eliminate the nitrogen essential to plants, and certain bacteria, acting as intermediaries, assist in its recapture. None of the higher forms of life could exist were it not for the unique ability of green plants to capture the radiant energy from sunlight and with it transform plain water and carbon dioxide into an organic compound which is basic to all others. Thus directly or indirectly the energy of the sun is the ultimate source of virtually all the energy dissipated in the activities of living organisms, as it is of nearly every other display of energy on the face of the earth. The processes of metabolism are complex, and much about them is still unknown. But they are the cornerstone of life.

The constructive processes of metabolism,

known as *anabolism*, result in the storage of energy or the manufacture of more protoplasm. Plants and animals are able to do these things by building the complex molecules of organic compounds, storehouses of energy that can be tapped when needed, and actual building materials of which the protoplasm itself is made. The variety and complexity of these substances is quite bewildering. Complex organic compounds are never found in appreciable quantities except as the products of living organisms. Thus one of the qualities of life seems to be its special ability to bank its wealth and to create its own form.

But these large and complex molecules cannot be built without cost, in the form of energy spent in the building. This cost involves the destructive activities known as *catabolism*. In any transfer of energy from one compound to another some energy is lost, in the form of heat or otherwise, and in this catabolic process energy leaves the protoplasm. Thus some of the energy already stored is constantly being released in various activities or in building more protoplasmic substance. Since in this perpetual series of changes some energy is lost, it soon would be a losing battle, were there not a periodic inflow of new energy as molecules of lower energy content leave. In animals, the energy is largely potential energy, held within the molecules of the food they take in; in green plants, it is largely the radiant energy of the sun's rays. The incoming energy is used through a multitude of chemical reactions, or chains of reactions, long and complex and and at present only partly understood. Anabolism and catabolism are the two closely inter-related aspects of this larger process.

Not all creatures possess this ability to build complex molecules to the same degree. Green plants start with much simpler raw materials than is possible for animals, and indeed, animals could not exist without the basic organic compounds which these plants produce. Had it not been for this ability to tap the virtually limitless source of radiant energy in the sun, life would never have gone beyond the formation of a few slimy films or discolorations within limited mineral waters where small amounts of available energy are present. This basic process, found only in green plants to any considerable degree, is known as *photosynthesis*, that is, synthesis by means of light.

Until quite recently, it was thought that animals could not put carbon dioxide and water together to form carbohydrates. It has now been demonstrated that, like plants, they can. But this synthesis, however else it may turn out to be the same, is basically and vitally different from the *photosynthesis* of the green plant, in which the energy of the carbohydrate originates in the sun's rays.

In other ways too the plant cell has greater powers of synthesis. It can make all the vitamins and the amino acids — the substances from which proteins are built — from inorganic molecules. The animal cell can make some amino acids from others, but many it cannot make at all. Thus the animal's diet must provide these so-called "essential" amino acids, and also the vitamins.

Yet despite these differences, metabolism is astonishingly similar in plants and animals. Carbohydrates, fats, and, to some extent, proteins are broken down to carbon dioxide (CO_2) and water (H_2O). Oxygen is consumed in this process, called respiration.¹ Even the many steps of respiration are essentially the same in all cells. So, too, are the syntheses of starch

(or glycogen, in animals) from sugars; fats from fatty acids and glycerol; proteins from amino acids; and the interconversion of one class of organic compound to another. Essentially similar, too, in plants and animals, are the catalysts which make all these metabolic changes possible.

Enzymes and Vitamins

These catalysts — that is, substances which further a chemical reaction but are not consumed in the reaction — are known as *enzymes* (Gr. *en* = in + *zyme* = leaven), so called because of the fermenting enzyme in yeast, which was one of the first to be investigated. It is now known that the precise and rapid way in which chemical reactions are steered into channels necessary for the maintenance of life would be impossible without these biological catalysts. Enzymes are extremely complex, being apparently protein in nature and (significantly) produced only in living cells. There are a great many different enzymes, a specific enzyme being required for each step in metabolism. To take just one example, a fairly simple metabolic process like the oxidation of glucose to CO_2 and H_2O in the release of energy would involve the action of at least twenty different ones! In a sense, the system is much like the assembly line in modern industry, where each worker does just one separate job. First one enzyme and then the next does its job, on down the line. Moreover, it is interesting, and from an evolutionary point of view significant, that the same enzymes appear to be present in the cells of both animals and plants. In spite of its immense variety, all life is very much alike in many surprising ways.

Most enzymes inside the cell seem to be composed of two parts, one protein and the other much simpler in chemical structure. These simpler substances are often *vitamins* (Lat. *vita* = life + *amine* = from ammonia), so called because it was once supposed that ammonia was important in their composition. Among the vitamins, B_1 , B_2 , and several others are the non-protein parts of different

¹ All cells respire in this fashion, even the green cells of plants during the daytime, where the nature of the gas exchange is reversed. Because of the preponderance of photosynthesis over respiration in these cells, CO_2 enters the cell as oxygen leaves. In the non-green cells of the plant, as in animal cells, oxygen constantly enters the cell as carbon dioxide leaves.

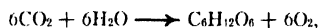
vital metabolic enzymes. But unlike the enzymes, or the protein parts of them, the vitamins required by a particular species of animal cannot be produced by its own protoplasm and must be obtained from other organisms which can synthesize them, usually and eventually plants. The vitamins, then, appear to be essential to certain metabolic activities in plants as well as animals.

THE ORGANIC COMPOUNDS IN PROTOPLASM

With their enzymes and vitamins as spark plugs, living cells are able to synthesize the main types of organic compounds — the carbohydrates, proteins, and fats — which serve them for the storage and conversion of energy and for building materials. All the organic compounds in all the protoplasm of most plants and all animals are ultimately derived from a simple carbohydrate, produced by green plants in photosynthesis.

Photosynthesis

While the first and last steps of this process can be summarized by the equation



this formula gives only the vaguest notion of the long chain of enzyme-sponsored reactions by which carbon dioxide and water are transformed into the basic energy-giving substance, a simple sugar, rich in potential energy. The exact nature of this first organic substance is still not clear, but ultimately glucose, a simple carbohydrate, is produced from it. Through the use of tracer elements, either isotopes or radioactive atoms, biochemists have been able to trace absorbed compounds or the products of their disintegration. It has thus been shown that the carbon dioxide is reduced to carbohydrate and the water is oxidized to oxygen. Reduction involves the addition of hydrogen; oxidation the removal of hydrogen. When hydrogen is added to CO_2 , carbohydrate is formed. When hydrogen is removed from H_2O , oxygen is left. This oxygen is liberated as free gas. While many steps of the process

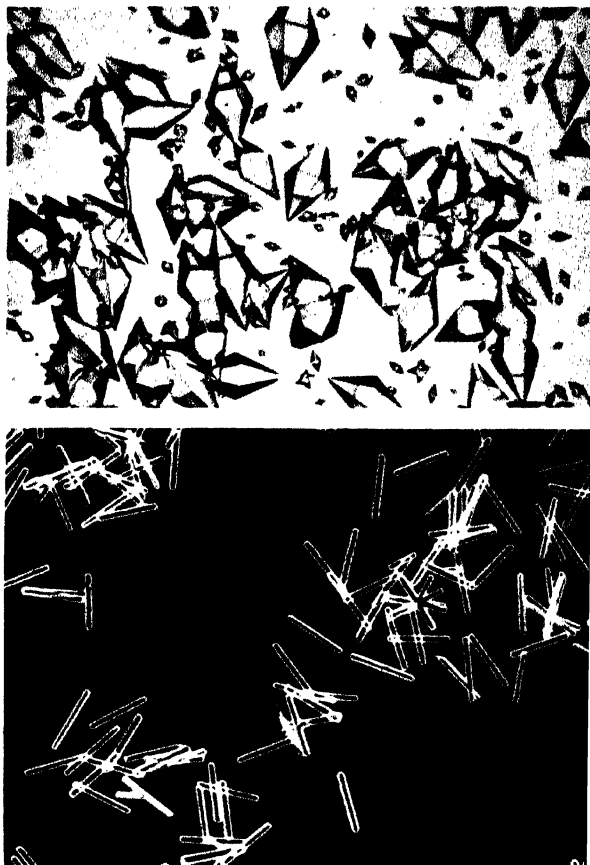


Fig. 43. Photographs of enzyme crystals, pepsin (above) and trypsin, enzymes of central importance in digested processes. These photographs were made by J. H. Northrop of the Rockefeller Institute.

are still far from clear, it is yet basic to the formation of higher organic compounds.

Chlorophyll. Essential to photosynthesis is the green substance in the leaves of plants, the green chlorophyll, which absorbs light and seems to be a part of an important enzyme. Chlorophyll absorbs light rays from sunlight, primarily in the red-orange and violet-blue regions of the spectrum. This leaves a mixture of unabsorbed light waves, especially in the green-yellow range, which accounts for the green color of light after passing through chlorophyll. The efficiency of photosynthesis is low at best. Maximum absorption could be achieved only if the leaf were able to absorb light from all wave lengths instead of only from selected bands, and maximum efficiency would result

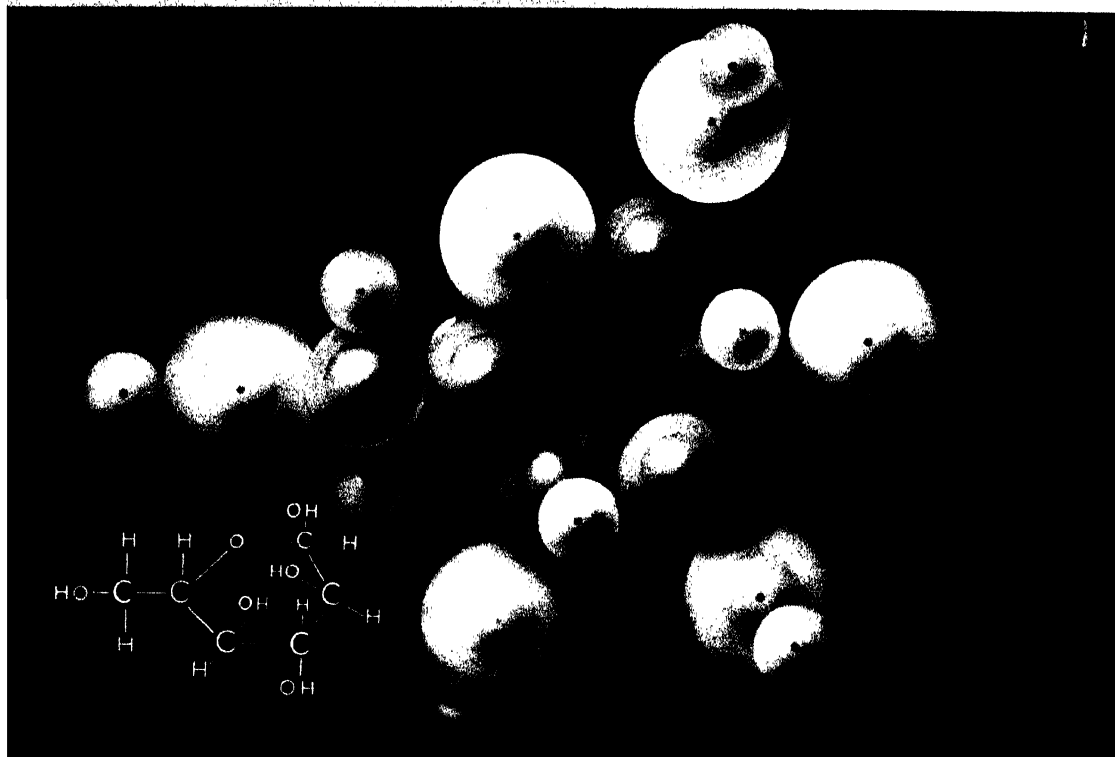


Fig. 44. A "typical" glucose molecule (diagrammatic).

only if it could transform the radiant energy into chemical potential energy with the loss of the least possible amount of heat. Visualize a cold, dank forest (heat loss is inefficient), growing at many times the speed of modern vegetation, with all its leaves dead black, and it becomes apparent what maximum efficiency might produce.

Although chlorophyll was named by Caven-
tous and Pelletier as far back as 1810, it was
not isolated until 1912, when the German
chemist Willstätter found that it is actually a
mixture of two very similar substances, chlo-
rophyll A and chlorophyll B. The formulae
for these are given as $C_{55}H_{72}O_6N_4Mg$ and
 $C_{55}H_{70}O_6N_4Mg$ respectively. Notice how little
the two differ, and especially note the presence
of magnesium (Mg) in each. This single atom
may be decisive to the amazing power of chlo-
rophyll. Magnesium, the only metallic atom
in the molecule, occupies a central position
in a complex ring. Another remarkable fact
about it, perhaps of great evolutionary sig-
nificance, is that a slight change in the struc-

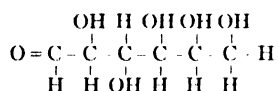
ture of the chlorophyll molecule, mainly in-
volving replacement of the magnesium by
an atom of iron (Fe), results in a compound
of great importance in the animal world,
namely *heme*, the pigment in hemoglobin,
which is the red coloring matter in blood.
Chlorophyll combines with a protein in the
cell to form a chlorophyll-protein complex pre-
sumably of enzymatic nature. Heme com-
bines with a protein to form hemoglobin.
The fact that the chlorophyll and the heme
both are combined with proteins in the cell
is perhaps another indication of their rela-
tionship. Still another may be the fact that
iron is necessary for the synthesis of both the
hemoglobin and the chlorophyll. Of course
it is a part of the hemoglobin molecule, but
it is necessary for the synthesis of chlorophyll,
where apparently it acts as a catalyst. It is
not likely that this similarity between chlo-
rophyll and hemoglobin are matters of pure
chance. (Rather, it is probably due to the
divergent evolution of a common compound
when the animal and plant kingdoms divided),

Carbohydrates

By photosynthesis, then, green plants are able to take carbon, hydrogen, and oxygen, and through the action of chlorophyll to convert the kinetic energy of sunlight into the high potential energy of a simple carbohydrate. In the process, chlorophyll forms intermediate compounds, but these soon break down again and release the chlorophyll in its original form in a manner typical of catalysts generally. The end products are glucose, $C_6H_{12}O_6$, and oxygen, O_2 . The oxygen is released into the air as a waste product.

But the glucose becomes the foundation of a virtually unlimited array of other organic compounds. A rich store of potential energy, it may be converted into starch for storage or into the cellulose of which the lifeless cell walls of plants are composed. Or, together with other compounds, such as salts, fragments of it may be converted into more complex organic substances, proteins and fats. The energy of still other glucose molecules may eventually be released in catabolism and used in the synthesis of organic compounds. In a great variety of ways, it becomes the basis for further compound formation, the basis for the metabolism of all organisms.

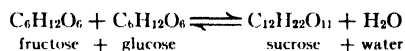
The simplest carbohydrates are the simple sugars, such as glucose, fructose, and galactose. All of these are built around a chain of six carbon atoms and may be represented by the simple structural formula $C_6H_{12}O_6$, or by the stylized structural formula



although in each of these compounds the various atoms are arranged in different ways (Fig. 44).

These simple compounds then combine with each other to form "double sugars," or disaccharides, such as sucrose or maltose; and then "multiple sugars" or polysaccharides, such as starches and cellulose. These are all convenient substances for the storage of energy

or for structural purposes. In general, the larger the saccharide molecule, the less soluble it is and the more useful as a building material. All these transformations are extremely complex, and cannot here be traced in detail. In a highly simplified version they may in general be described somewhat as follows:



The important thing is that these large molecules may again be broken down, by a process which is essentially the reverse of this, into simple sugars available as immediate sources of energy. Indeed, both processes are extremely flexible.

The complexity of the breakdown of these substances may be illustrated by what happens in animals. Animals digest polysaccharides to disaccharides and these to monosaccharides in the digestive tract under the catalyzing influence of enzymes of the saliva, pancreas, and intestine. The resulting monosaccharides are absorbed into the bloodstream and by this avenue reach the cells of the body. Especially in the liver, the polysaccharide glycogen is formed under the influence of at least three different enzymes. This compound is relatively insoluble, and reduces the quantity of soluble sugar in the blood. As bodily activity reduces the amount of blood sugar, the glycogen is converted back into monosaccharide in the liver under the influence of other enzymes. This replenishes the blood sugar. For elucidating the chemistry of the glucose-glycogen story, Carl F. and Gerty T. Cori were recently awarded the Nobel Prize in medicine.

Proteins

There are many different carbohydrates, but there is an enormous number of proteins. Not only are these the most complicated of the organic substances, they are the most important in building protoplasm. In addition to their crucial role in maintaining metabolic processes, they are primarily responsible for the stamp of individuality that marks each class, each species, and even each individual as distinct from every other. In addition to

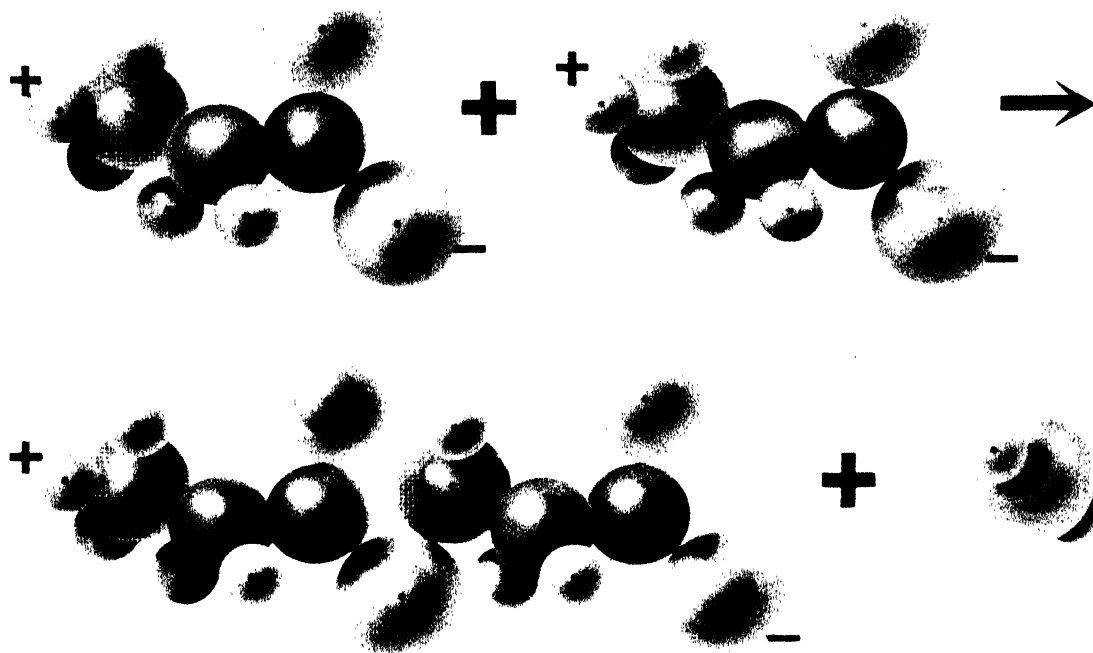


Fig. 46. Formation of a simple dipeptide, glycyl-glycine, and a molecule of water from two ionized molecules of glycine (see Fig. 45).

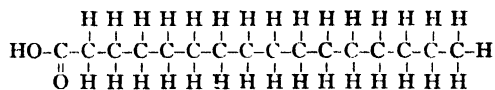
ualized proteins of all, the autocatalytic nucleo-protein genes.

But animals do not limit their intake of proteins to their structural needs. Indeed this would be almost impossible, for certain proteins would have too many of one amino acid and too few of another. Thus, if fed adequately, they will have an excess of some. These are not lost, but are converted into other compounds by removal of the amino radical while the remainder of the molecule may then be converted into glucose and used as a source of energy. The NH_2 may then be converted into a nitrogenous waste, such as urea $\text{CO}(\text{NH}_2)_2$, which is eliminated.

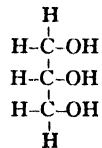
Fats (Lipins)

The third great group of organic compounds includes the fats and fat-like substances, primarily of value in the storage of energy, though they also play an important structural role. For fat-like substances, such as phospholipins and sterols, are essential in maintaining the colloidal organization of protoplasm and its membranes.

True fats are complex molecules composed of two substances known as fatty acids and glycerol. Fatty acid molecules may be visualized as long chains of carbon atoms with only hydrogen atoms attached except at one end. There appears the familiar carboxyl radical found also in amino acids. One of them, palmitic acid, may in structural formula be pictured as something like this:

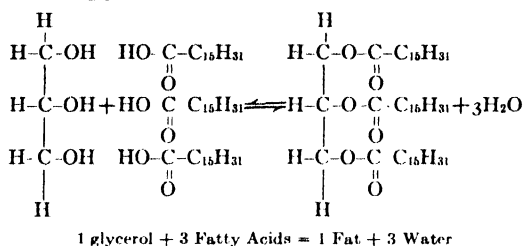


A molecule of glycerol, the other substance, may be represented something like this:



These two substances are joined by a complicated chemical reaction known as dehydration synthesis to become, essentially, fuel compounds. Under the sponsorship of suitable enzymes, each H of the carboxyl radical of the

fatty acid combines with one of the OH groups of the glycerol, somewhat as follows:



Thus a molecule of fat is formed. It may be transformed back into fatty acid and glycerol by the reverse process, hydrolysis, and these compounds may then be oxidized to release energy. Since energy is released by oxidation, and since fats contain much less oxygen in their original structure than carbohydrates, fats have a higher fuel value per unit of weight than any other food. Because of this, and because they are insoluble in water, they are ideal for the storage of energy and are so used by animals generally.

Organic Substances and Life

These organic compounds, together with water, salts, and many other substances, form protoplasm, and the complexity of the interaction among them is almost inconceivable. Many proteins combine and recombine with inorganic ions, and may combine with phospholipins or fragments of hydrolyzed fats. Glucose and other carbohydrates combine with phosphates. Water, far from being simply a solvent and a carrier, constantly interacts chemically with the substances dispersed in it, not only in hydrolysis and dehydration synthesis, but in many other ways as well.

All these processes and relationships, delicately and specifically adjusted to one another, together produce life, and it is not always possible to be sure whether a compound is an essential part of protoplasm or merely a fuel or even a waste product. At best, however, such a distinction is more or less artificial. Because of its dynamic nature, protoplasm without fuel is impossible. Nor could it exist without the amino acids essential to the structure of necessary proteins. Yet it would be

meaningless to call any one part of the protoplasm, or any one compound in it, alive — even the genes or other autocatalytic enzymes which reproduce themselves. For not one of them can live alone or do what protoplasm as a whole can do. They are merely the components of a physico-chemical system which only in its totality possesses the full properties of life.

But since not all life is alike, it is not enough for the substances to interact and be alive; they must be alive in specific ways. The protoplasm of a geranium is alive, and so is that of an oak. A cell within the human brain is alive, and so is one in the fin of a fish. Basically the processes which take place in all the many kinds of cells are alike, though the cells are obviously not interchangeable, and an attempt to substitute one type for any other would yield most unsatisfactory results. Although there are common principles in the structure and behavior of all living things, the intricate business of being alive demands much more than this. Each organism, largely by virtue of a nucleus of unique self-perpetuating catalysts, gives the basic life functions subtle differences that produce the distinction between geranium, oak, brain, and fin.

NUTRITION

Holophytic Nutrition (Plants)

Metabolism, occurring in each cell of the body, is dependent on the constant inflow of substances into the organism. The intake of these substances, and their conversion and use, is *nutrition*. In its broadest sense, nutrition would include metabolism, the change of these molecules inside the cell, and also the elimination of the resulting waste molecules. In its narrow sense, it would include the fate of the molecules from the time of entry into the organism until they entered the cell to take part in metabolism.

From what has already been said about plant metabolism, it is clear that nutrition in green plants is very different from that in animals. There is no digestive tract. The incoming

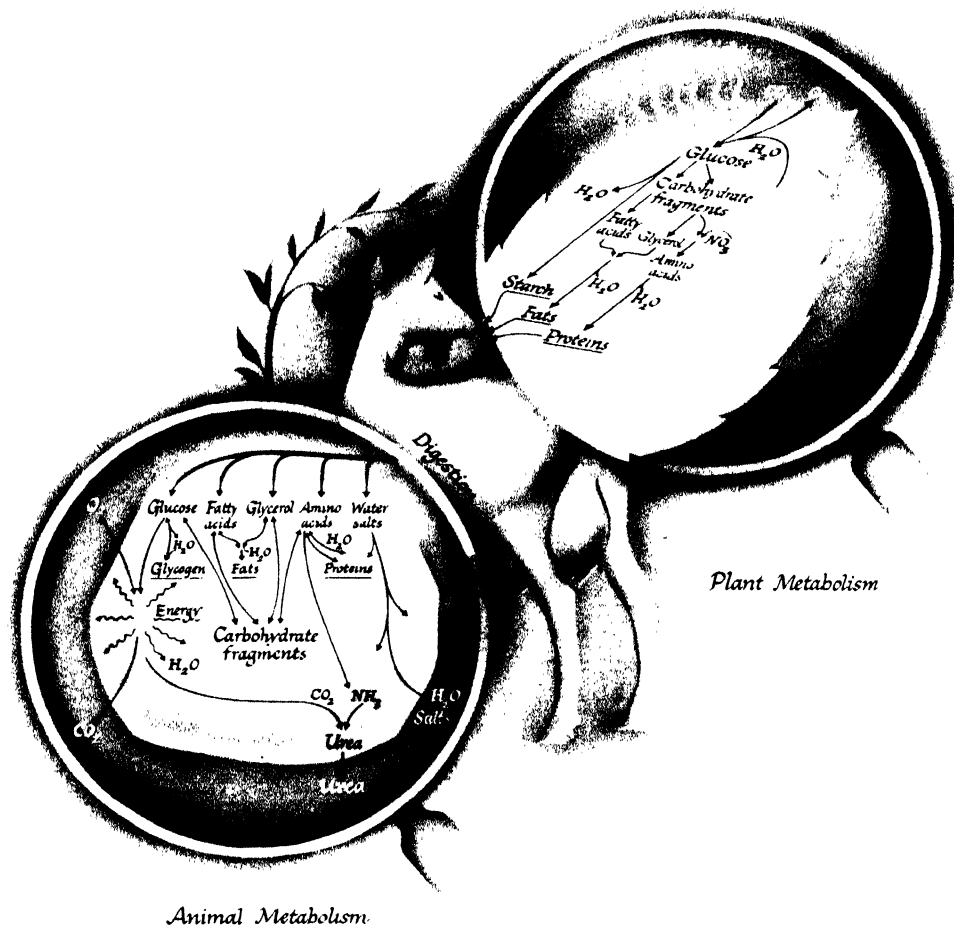


Fig. 47. The scheme of animal and plant metabolism.

molecules are already in soluble, diffusible form. They are mainly simple inorganic molecules, with which the plant builds its organic substances. In this sense then, the green plant is not dependent on other organisms for energy-rich food molecules; its nutrition is therefore *autotrophic*, that is, self-nourishing. Since there are some non-green autotrophs, the metabolism of green plants is more specifically called *holophytic*, that is, "wholly plant-like."

The central theme of holophytic or green-plant nutrition is photosynthesis, which results in the formation of the carbohydrate glucose.

From this organic compound, together with the water and its dissolved freight of salts which the plant absorbs from the soil, the plant manufactures a multitude of complex organic compounds. Although green plants stand almost alone in the ability to use radiant energy efficiently in the accumulation of chemical potential energy, other plants and to some degree animals, too, share with them the ability to synthesize many other complex organic compounds from simpler ones. Thus the various conversions of compounds from monosaccharides to polysaccharides, from

amino acids to proteins, from fatty acid and glycerol to fats, as well as conversions of carbohydrates into fats and into amino acids, which plants perform, are also performed by other organisms. However, as we have seen, green plants are autotrophic. They can perform all the syntheses outlined, can make all kinds of amino acids, all necessary vitamins and fats. Furthermore a plant begins life with but a minute fraction of the chemical potential which it leaves when its individual life ends, and in the typical green plant this is wholly produced within the plant through the conversion of radiant energy. In brief, anabolism in plants greatly exceeds catabolism, and the intake of carbon dioxide exceeds its output, while oxygen is liberated.

These statements all refer to the plant as a whole, but actually only a portion of the plant is in a position to absorb sunlight. In trees, the cells of the twigs, trunk and roots are in eternal darkness, and yet these too must constantly maintain their metabolism. The energy within such cells is obtained from the oxidation of organic compounds produced in the green leaves, so that in these non-green tissues catabolism must exceed anabolism, as it does in animals, and oxygen is consumed while carbon dioxide is liberated. During the night, all plant tissues follow this pattern.

In simple terms, the overall process of green plant metabolism may be summarized as follows: light streams upon the leaf, and its energy is absorbed by chlorophyll. Carbon dioxide diffuses from the air into the leaf through its pores. It is supplied with water and inorganic salts absorbed by the roots. Through the enzymatic activity of chlorophyll and with the radiant energy it has absorbed, hydrogen is removed from some of the water, and combines ultimately with the absorbed carbon dioxide to produce glucose. In the process, oxygen is released as a waste product and escapes back into the air. Glucose may be synthesized into starch and stored, or into cellulose to be used as a structural substance. And the energy of glucose is released in catabolism and used in synthesizing fats and proteins.

This meager description indicates only a few of the main steps in the intricate flow of chemical interaction that constitutes plant metabolism, and in a sense, the essence of plant life. Each chemical reaction must be attuned to all the others in the cell if a dynamic balance is to be maintained. Governing these multitudinous activities are the organic catalysts or enzymes, each of which directs a specific change; and they in turn are under the control of the genes, which maintain the ability to duplicate themselves at the proper time and in the proper place.

Holozoic Nutrition (Animal)

The essential difference between the nutrition of green plants and that of animals is that the latter do not themselves synthesize most of the substances which provide them with energy, but get these substances in the form of foods—chemical compounds stocked with potential energy, which is then either transformed into kinetic energy utilized in the activities of life or is used in the synthesis of organic molecules which become parts of the protoplasm. Typical animal nutrition, in which energy-containing organic foods are ingested, is called *holozoic*. It is the type of nutrition in which the creature appropriates supplies of energy accumulated by other organisms, either plants or animals, though ultimately all animals depend on plants for many of the organic substances they need. Moreover, because during the day photosynthesis dominates respiration in the green plant but is absent in the animal, the daytime gas exchange is reversed. Thus while plants take in carbon dioxide and give off oxygen during the day, animals are always taking in oxygen and eliminating carbon dioxide.

The food of animals must supply them with all the requisite energy (calories), proteins (or at least the amino acids from which to make proteins), and vitamins. As we have seen, plants build amino acids from simple inorganic substances. Animals cannot do likewise. They can, however, make some of the thirty-odd amino acids through the rearrangement of

other molecules. But nine or ten cannot be produced even in this fashion. These "essential" amino acids must therefore be in the diets. With very few exceptions, animals cannot synthesize molecules like thiamin, riboflavin, and ascorbic acid. These vitamins must also be obtained from the food.

Notable in animal metabolism is its dependence on certain synthetic powers of other organisms. They have shaped their metabolic economy to an abundant supply of potential energy in the form of food. Consider an analogy. Suppose a person were to obtain his household fuel and furniture by commandeering the furnished homes of others. He would sort and allot. Fuel would be used for fuel, furniture parts for replacement and repair. But since these materials would be obtained in indiscriminately mixed lots, he would often have to take too much furniture, for example, in order to get enough fuel. Rather than throw the furniture out entirely, he would proceed to chop it up, remove valuable fittings only to discard them, and burn the rest for fuel. If this sounds wasteful and profligate, it is meant to. This is precisely what animal organisms do. Complex amino acids taken in beyond they are deaminized or deprived of their amino radical (NH_2) and otherwise altered, to be transformed ultimately into a monosaccharide and used for fuel. The nitrogenous waste is eventually excreted, and oxygen is consumed while carbon dioxide is given off.

Saprophytic Nutrition (Fungi and Bacteria)

Between holophytic and holozoic nutrition there are many intermediate forms that lead in a virtually unbroken graded sequence from one extreme to the other. Those organisms completely dependent for food on a living host are called *parasites*. However, most intermediate forms of nutrition are referred to as *saprophytic* (Gr. *sapros* = rotten) since their activities either cause or thrive upon decaying organic matter. Since saprophytes are not autotrophic but require organic compounds produced by other organisms for energy, they are in this sense animal-like. But many sapro-

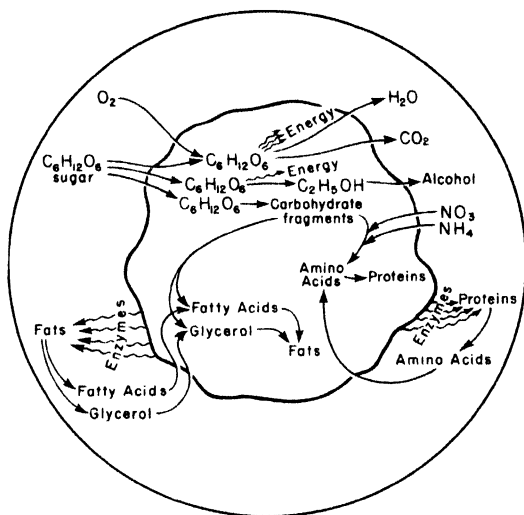


Fig. 48. Saprophytic metabolism. Yeast, bacteria, or mold cultures, showing food exchange.

phytes have powers of synthesis exceeding those of animals, and some almost equal plants in this ability. In this sense saprophytes are plant-like (Fig. 48).

Saprophytic nutrition is found in yeasts, molds, and other fungi, such as toadstools and mushrooms. It is also found in certain forms of degenerate seed plants, such as the ghostly, glistening white Indian pipe. Most bacteria, too, are saprophytic, and perhaps this group shows the nearest approach to the original type of nutrition. Generally, saprophytes simply absorb from their environment those soluble organic molecules which they require. They may obtain these by living among the disintegrated tissues of dead organisms that have been partially digested by other saprophytes. Or they may themselves produce enzymes capable of transforming large insoluble organic molecules into smaller soluble ones which can be absorbed. We shall make the closer acquaintance of all these organisms in later chapters. Only their mode of nutrition and their role in the metabolic economy of nature concern us here.

Molds. Molds, such as the bread mold *Rhizopus nigricans*, or the green mold often seen on oranges, *Penicillium*, are delicate organ-

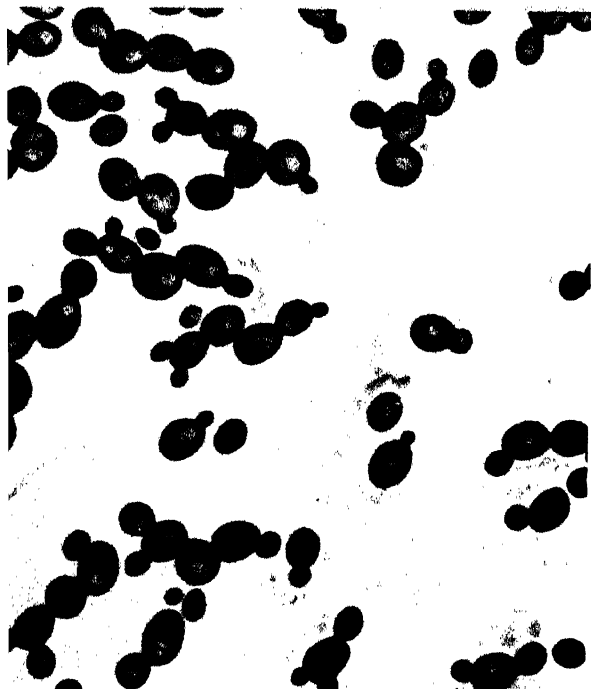


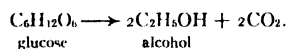
Fig. 49. Budding yeast plants.
Each plant is a single cell.

isms like plants in structure and in metabolism generally. Lacking chlorophyll, however, they obtain their energy in the form of organic compounds, such as sugar, which they absorb through a network of fine silken hairs which penetrate the substrate on which they grow. Enzymes produced by these threads, the mycelium, hydrolyze the starch of bread, for example, into soluble sugar which is then absorbed. In its remaining aspects the metabolism of these organisms is much like that of green plants, for in both, amino acids and proteins are synthesized from carbohydrates and the nitrates absorbed from the substrate. Molds frequently cooperate or compete with bacteria in reconvertng organic compounds — which are unavailable to green plants — into inorganic form, thus playing an important, in fact an essential, role in nature's economy. This enforced competitive relationship with bacteria appears to have guided the evolution of such abilities as that of the mold *Penicillium* to produce such an effective anti-bacterial substance as penicillin.

Yeasts. Equally plant-like in metabolism and

of considerable economic importance are the many varieties of yeasts (Fig. 49). These are either single celled plants or small clusters or colonies, but they are singularly plain in appearance and offer little to attract the eye. Like the molds and their reproductive cells, the spores, they are ubiquitous, and hence no sweet or starchy solution can long remain exposed to air without beginning to "work" or ferment as a result of the activity of yeasts. Like molds they obtain energy by absorbing some form of sugar from the medium in which they live, and like all other organisms they require other atoms in addition to the carbon, hydrogen, and oxygen of which sugar is composed. In other words, yeasts cannot grow in solutions of pure sugar. Like plants, and unlike animals, yeasts generally secure their nitrogen in inorganic form, and with sugars synthesize it into amino acids and finally into proteins. Yeasts, however, generally secure their nitrogen in the form of ammonium salts (NH_4^+) rather than in nitrates (NO_3^-) as do most plants.

Yeasts possess the ability, shared by a few other organisms such as some bacteria, of carrying on their metabolism entirely in the absence of free oxygen. Instead of oxidizing sugars to carbon dioxide and water for the purpose of releasing energy, they can transform sugar into alcohol and carbon dioxide:



This process of alcoholic fermentation is called *anaerobic* (Gr. *an* = without + *aero* = air + *bios* = life). Since yeast does not flourish under anaerobic conditions, and the waste product, alcohol, soon puts a stop to further activities, this form of metabolism appears to be merely an emergency measure. In the presence of oxygen, yeast grows and reproduces rapidly, since oxidation yields considerably larger quantities of energy from similar amounts of sugar than does anaerobic fermentation. But it is because of their ability to transform sugar into alcohol and carbon dioxide that yeasts are of great economic importance. The uses of alcohol are well known, and the liberation of carbon dioxide makes yeast useful as a leaven

in bread making. Since yeasts cannot generally utilize starch because they lack the necessary hydrolyzing enzyme, they cannot be used to produce alcohol from grain, potatoes, or other starchy products unless starch-splitting enzymes, abundantly present in sprouting plants, are added. Recent experiments in the mass production of certain varieties of yeasts indicate that they may in time become an important source of staple food rich in necessary proteins and vitamins.

Saprophytic Bacteria. Although bacteria are generally classified with the plants, their forms of nutrition are almost as numerous as their kinds. Although they are an essential link in the scheme of life, man is in constant active competition with them. Not only do they compete for available food supplies but they constantly seek to attack and destroy man's plant and animal food producers and even his body.¹ Yet bacteria are essential to life, for without them nitrogen and other elements necessary to the growth of green plants would not be returned to usable inorganic form and would remain forever locked up and inaccessible. The process by which this decomposition occurs is called decay or, where proteins primarily are involved, putrefaction. In putrefaction, proteins are converted into amino acids, into split proteins, often poisonous, called ptomaines, and into many other compounds, some (like hydrogen sulfide and ammonia compounds), being volatile and of offensive odor. Many of these substances, if not metabolized by the bacteria producing them, are further dismantled by other bacteria until finally only simple, inorganic compounds remain.

By virtue of these powers of chemical dissolution, bacteria become serious competitors and dangerous foes as well as essential benefactors. The vast sums spent annually in canning, in refrigeration, and in other efforts to preserve foods and prevent decay are a kind of tribute paid to the bacteria and the molds in return for the indispensable services

they render in other ways.

In some cases, the chemical powers of certain bacteria are employed directly in producing substances useful or desirable. The fermenting of sauerkraut, the souring of milk, and the transformation of alcohol into vinegar are useful forms of decay in which molecules other than proteins are degraded. Modified or controlled forms of putrefaction are also employed in cheese making, in sewage disposal, in oil refining, and in the tanning of leather. Thus guided into suitable channels, the activities of bacteria are useful and essential, much in the manner of other "forces of nature." Like many such forces, they are both a blessing and a curse as far as mankind is concerned.

THE FOOD CYCLES

In a world of keenest competition, no available source of energy or raw material is long left without a taker. Thus the waste products of one organism (if not the entire organism) become the source of energy and raw material for another, and so on in endless cycles by which the essential elements are continuously made available to all living forms.

The Nitrogen Cycle

One striking evidence of this interdependence of various forms of life is to be found in the so-called *food cycles*, in which two essential elements, nitrogen and carbon, are recaptured and handed around in an unbroken circle from creature to creature (Fig. 50).

Nitrogen is of course essential in the composition of every living organism, since it enters into the structure of the all-important proteins. But since most plants can utilize only the proteins they themselves have built from the inorganic nitrogenous compounds they find in the soil and transform into proteins, the time would soon come when the nitrogen content of the soil fell below the minimum needs of the plant if this supply were not somehow replenished. Should this

¹ For a discussion of bacterial diseases, see Chapter 23.

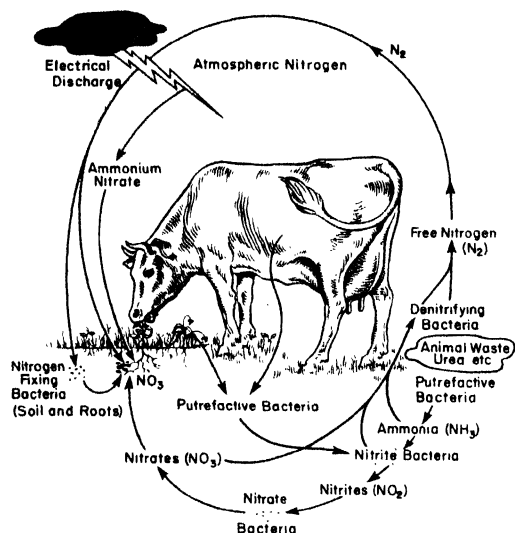


Fig. 50. The nitrogen cycle.

happen, the growth of plants would be stunted and their leaves would turn a sickly yellow, or they would fail to grow at all, despite the fact that they are bathed in an atmosphere four fifths of which is nitrogen. Such a plant would be in much the situation of the shipwrecked mariner dying of thirst on an ocean of water. This problem is by no means purely hypothetical. A garden from which crops are annually removed soon "runs out" unless the minerals of the soil are replenished. This may — indeed in modern culture must — be done by applying chemical fertilizers. In nature, where crops are not actually removed, this is achieved by on-the-spot conversion of complex compounds into simpler ones again, through the activity of bacteria in the nitrogen cycle.

The cycle begins with the nitrates which are a primary source of nitrogen for plants and are converted into amino acids and proteins. When a plant dies, its protein treasures will be left unguarded by the vital processes of the living protoplasm, and will at once be attacked by multitudes of molds and bacteria. Or an animal may step in and eat the whole plant, either living or dead, thus temporarily thwarting the efforts of the bacteria. But in

the end the putrefactive bacteria in the soil get the proteins or their products, either when the animal dies or when it breaks down the amino acids taken from the plant and excretes the nitrogenous element as urea. The putrefactive bacteria excrete most of the nitrogen thus obtained as ammonia (NH_3). The ammonia or ammonium compounds serve as a source of energy for other soil bacteria, the nitrite bacteria, which oxidize them and excrete nitrites (NO_2), which are oxidized further to nitrates (NO_3) by nitrate bacteria, thus completing the cycle.

It is evident from this description that the "nitrogen cycle" is actually a series of interrelated, partly interlocked, partly alternative cycles. The plant may be decomposed by putrefactive bacteria directly, or it may be eaten by an animal and its amino acids incorporated in it, or deaminized and excreted. The ammonia produced by putrefaction may participate in the metabolism of a sequence of other bacteria, or it may be utilized by some plants directly. The cycle may be "broken" by the liberation of free nitrogen, for certain denitrifying bacteria act on ammonia, nitrites, or nitrates in such a way as to release nitrogen (N_2) into the air.

"Lost" nitrogen may be returned to the cycle again by numerous means. On the roots of leguminous plants, and scattered through the soil, are bacteria (Fig. 51) such as *Rhizobium*, which utilize the energy of absorbed organic compounds to oxidize free atmospheric nitrogen to nitrates for further metabolic uses. These nitrogen-fixing bacteria thus help to restore the escaped nitrogen to the cycle. Some forms of the mold *Penicillium* and certain blue-green algae also have this power.

Non-biological processes also play a vital role in supplementing the available nitrogen supply. Electrical discharges during thunderstorms produce appreciable amounts of nitrogenous compounds estimated to be as high as five pounds per acre per year. Less important is the evaporation of water which may dissociate, allowing part of its hydrogen to combine with nitrogen to produce ammonium nitrate.

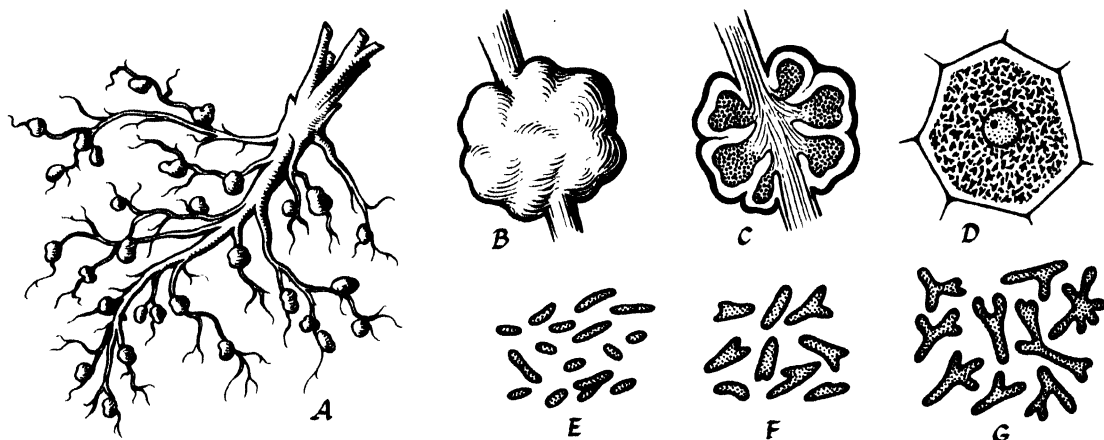


Fig. 51. A. Legume root with nodules of nitrogen-fixing bacteria. B and C. Outer view and section of nodule. D. An enlarged nodule cell containing bacteria. E, F, and G. Bacteria, greatly enlarged.

Modern mechanized farming on the tremendous scale practiced in the United States today would be all but impossible without the so-called chemical fertilizers rich in nitrogen, and without these compounds the world would be far hungrier than it is. Nitrogen compounds on such a scale are not readily available from natural sources such as the guano deposits of sea birds and of bats. Since the turn of the century attempts have been made to tie atmospheric nitrogen into usable compounds, and these were gradually perfected until now several million tons of ammonia are produced annually. The most important and economical of these processes is the Haber process, in which nitrogen and hydrogen are forced to combine under pressure in the presence of a catalyst: $\text{N}_2 + 3\text{H}_2 \longrightarrow 2\text{NH}_3$. Once the ammonia has been produced, further transformation into other compounds is a relatively simple matter. In this way modern man helps to keep the vital nitrogen cycle closed, although he flagrantly disrupts it in the way he disposes of organic refuse and sewage. In ancient cultures, such as China, where nitrogen fixation was never practiced, fertility of the soil could be maintained only by the most careful and scrupulous conservation of all animal and human excrement. If the cycle cannot be restored, it must not be broken.

The Carbon Cycle

A similar relationship exists between different organisms with respect to another vital element, carbon. It is an astonishing fact that carbon, the backbone of all organic compounds and hence of life itself, is found in available form only in relatively minute quantities (Fig. 52). Normal air contains only about .035 per cent of carbon dioxide by volume. From this mere trace of carbon dioxide, only three elevenths of which is actually carbon, plants must obtain virtually all their carbon, and in turn become the source of carbon for all other organisms. It is little short of miraculous that they should be able to do so.

The magnitude of this assimilating process becomes clear from some numerical estimates. To manufacture the complex carbohydrate cellulose of which it is composed, a tree of average size requires as much carbon dioxide as is contained in about twelve million cubic yards of air, or about thirty thousand times the volume of air in an average-sized classroom (25 by 40 feet). It has been estimated that an acre of potatoes would have to extract all the carbon dioxide in the air above it to a height of well over a mile in order to produce its crop — assuming, of course, that the air directly above the potato field never changed. A leaf area of about one and a half times the

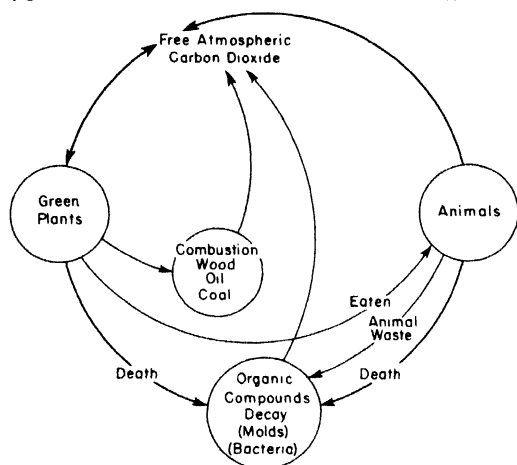


Fig. 52. The carbon cycle.

floor area of the average classroom would be required to absorb and use the amount of carbon dioxide given off by the average man in twenty-four hours. Conversely, since a molecule of oxygen is released for each molecule of carbon dioxide absorbed, a similar leaf area would be necessary to supply the average man with the oxygen he requires in a twenty-four-hour period. Again, if all the organic matter produced by this assimilation of carbon dioxide could be utilized by a man, this amount of leaf area would be able to supply the energy needs of one human being. Actually, more would be necessary, since he could not utilize all the compounds thus formed and since he needs compounds for other purposes than energy.

Here an interesting relationship suggests itself. The total lung area of a man is comparable in extent to the leaf area required to keep him alive. Perhaps this might be expected, since his lungs must accommodate an amount of gas exchange equal to that which takes place in the given leaf area. The sources of free carbon dioxide are preponderantly organic. Animals breathe it out, decay organisms give it off, and even organic compounds millions of years old, such as coal and oil, release it when burned. The only way in which this carbon dioxide may find its way back into the organic cycle is through the activities of green plants.

Since carbon is usually returned automatically to the free air which knows no boundaries, local dearth of carbon, such as that experienced for nitrogen and other soil-borne elements, is unknown. Man needs no carbon-bearing fertilizers, for this essential element is free to all.

The Grand Scheme

While the metabolism of animals, plants, and other organisms may be studied as individual cases, the grand harmony of nature does not become apparent until the various forms of metabolism are seen in relation to each other. In fact, all of nature might be considered one gigantic integrated organism, each part of which depends on all the others. Animals could not exist without green plants, for these are their sources of organic nitrogenous compounds, required for protoplasmic structure, as well as their sources of energy in the form of the organic compounds carbohydrates and fats. Green plants, in turn, could not exist without the activities of the soil bacteria. These organisms transform complex organic nitrogenous compounds into the simpler inorganic compounds upon which green plants depend, and release the carbon dioxide locked within organic compounds so that the supply removed from the air is constantly being replenished.

Whether the animal organism is necessary to this cycle is perhaps doubtful. It is true that animals produce substances which can be converted into plant foods by bacterial action and that they return carbon dioxide into the air. But bacteria are equally capable of performing this role, so that a life cycle without animals is conceivable. Life cycles without bacteria are possible only in the laboratory, where the actions of bacteria can be artificially replaced by chemical processes in retort and crucible. Life cycles without plants are conceivable only on a miniature scale under very special conditions not frequently found in nature. Thus while animals appear less essential than any of the others, each type of organism plays an integrated part in the scheme of the whole.

The Cell: the Unit of Structure and Behavior

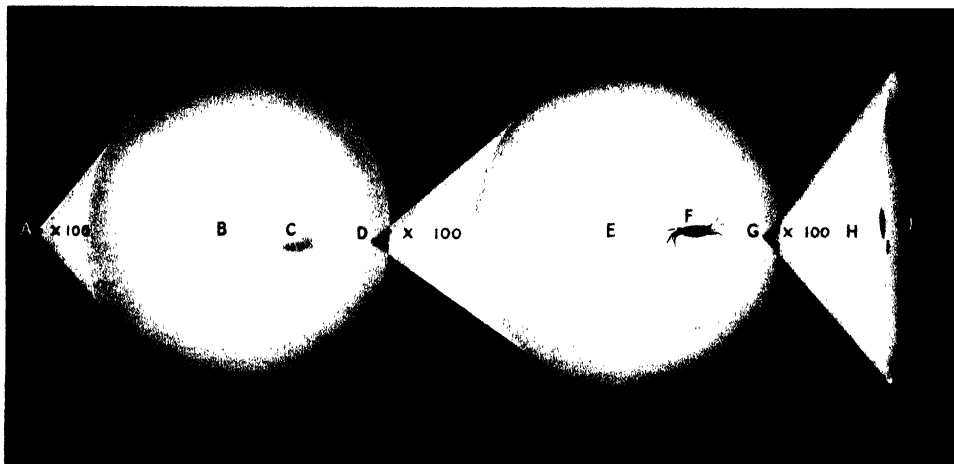
A Few Comparative Sizes

A small free-living animal, like an amoeba, can be seen with the unaided eye. The average cell is no larger than the finest visible dot that can be made with a needle-sharp pencil, about $\frac{1}{10}$ mm. in diameter.¹ One of the red blood cells in the human body, however, has only $\frac{1}{10}$ the diameter of an amoeba. A red blood cell, 7.5 microns in diameter, can easily be seen in any student microscope. Even some bacteria can readily be seen with the high-powered objective of an inexpensive microscope. Other bacteria are so small that only a powerful microscope

and skillful technique will reveal them. Were the virus that causes hoof and mouth disease in cattle magnified to the size of an amoeba, it would be 10,000 times larger than it is (Fig. 53). A man magnified to the same degree would tower 10 miles high. A toad's egg thus magnified would be as big as a house, or over 30 feet in diameter. At this monstrous magnification, *Bacterium pneumosintes* would still be no larger than a mustard seed. The viruses would range from about that size down to the barely visible, and the largest non-living organic molecules could scarcely be seen with the unaided eye. Without instruments for magnification, the study of the cell, the unit of protoplasm, would be impossible. Finally comes the realm of the truly invisible, small molecules

¹ 25.4 mm. = 1 inch. 1 mm. = 1000 μ = 1,000,000 m μ .
Terms: mm. = millimeter; μ = micron; m μ = millimicron.

Fig. 53. Size scales visualized. A. Toad's egg, natural size. B. Toad's egg $\times 100$. C. Amoeba $\times 100$. D. Red blood cell $\times 100$. E. Red blood cell $\times 10,000$. F. Typhoid bacterium $\times 10,000$. G. *Bacterium pneumosintes* to same scale, and (H) again $\times 100 = 1,000,000$. I. Virus of hoof and mouth disease to same scale. J. Large organic molecule to same scale.



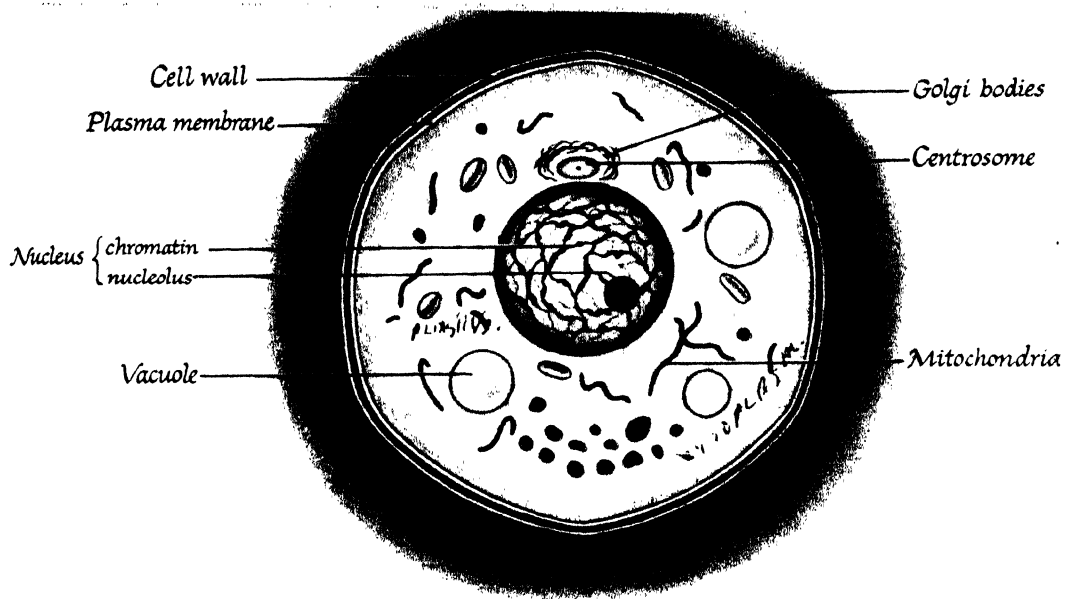


Fig. 54. Diagram of a "typical" cell.

and atoms, though by means of ionization chambers and other devices even these can be counted, weighed, and studied.

The Microscope

Cells were named in 1665 by Robert Hooke, who observed that a sliver of cork was made up of minute box-like structures which he termed *cellulae*. While today the term *cell* is applied not only to the inert housing which Hooke saw in cork but to the unit of living substance as a whole, nevertheless his discovery began a long series of studies leading to what is now known about protoplasm. A few years later, Anthony van Leeuwenhoek of Delft, Holland, discovered "wretched beasts" of unbelievable minuteness in the most diverse materials and objects. Under his eye came animals which consisted of but a single cell, the Protozoa, and he saw organisms even smaller than these, the Bacteria.

None of these discoveries would have been possible without the microscope. It was through Galileo, who himself invented neither the first telescope nor the microscope, that both instruments were applied to scientific ends and so became generally known about the

year 1610. Early records of microscopic research are very scant, but some fifty years after Galileo, around the year 1660, there appeared a considerable number of microscopists. Among them were such famous names as Marcello Malpighi, van Leeuwenhoek, Hooke, Jan Jacob Swammerdam, Nehemiah Grew, and others. These men laid the foundations of the modern concept of the structure and nature of living things. Three hundred years is a long time compared to the human life span, yet considering the vast amount of observation and knowledge amassed during this period, it is astonishingly brief.

The first microscopes were apparently simple lenses, crude indeed by modern standards. Compound microscopes—that is, microscopes using two or more lenses—were introduced by Janssen, but Leeuwenhoek preferred his own simple lenses which he ground from little beads of glass. One of his lenses, still in existence, is said to have a magnifying power of 270 diameters. Only later, when grinding and testing techniques were greatly improved, did the compound microscope give better results than the simple lens. The modern microscope uses lenses less than $\frac{1}{16}$ inch in

diameter, and these must be ground to a tolerance exceeding $\frac{1}{10000}$ of an inch. As a result of such improved technique in manufacture, it is now possible to achieve a magnification limited only by the length of the waves of light itself. Thus the modern optical microscope can achieve a magnification of considerably over a thousand diameters.

In recent years the ability to see minute things has been even further increased by the invention of the electron microscope. Organisms that approach the length of a light wave in smallness do not reflect such waves but scatter them, just as a rock or boulder lets ocean waves pass it by, whereas a sea wall reflects or throws them back. By using a stream of electrons, or more recently, protons, shadow images of objects quite beyond the power of an optical microscope, such as viruses, can be made visible either on a fluorescent screen or on a photographic plate. Thus pictures have been obtained of organisms that previously were merely suspected to exist. Some of these are even smaller than the largest organic molecules. Perhaps, too, the electron microscope will enable us to see individual genes.

CELL STRUCTURE

Surrounding most plant cells is a non-living and inert cell wall, though this is absent in most animal cells. Surrounding the protoplasm, but normally invisible in plant cells because it is pressed against the inside of the cell wall, is the living cell membrane, the outer layer of the protoplasm. Within this lies the mass of the cytoplasm which constitutes the bulk of the cell. Its composition varies from organism to organism, or even from time to time within the same organism.

Within the cytoplasm is a single spheroid body often quite clearly visible and of regular outline, but differing in shape in different organisms. This is the nucleus (Lt. nucis = nut, kernel) and it is of fundamental importance to the activities and to the very life of the cell.

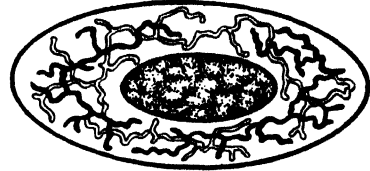


Fig. 55. Mitochondria in a living epidermal cell of a tulip petal.

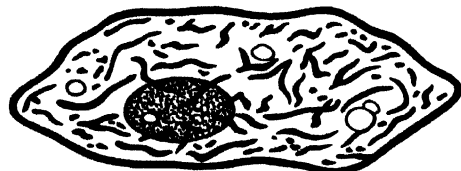
The Cytoplasm

Within the cytoplasm can be observed the various structures, the granules and droplets previously discussed, and in different parts of the cell the substance appears to have different viscosities, varying regionally from a stiff gel to a fluid sol.

The cytoplasmic granules have various sizes and shapes in different kinds of cells. Some of these have recently been studied intensively, and have even been isolated from the cell and, to some extent, analyzed biochemically. Larger ones, called mitochondria (Gr. *mitos* = thread + *chondros* = cartilage), are peculiar granular, rod-like or thread-like structures found in all cells (Fig. 55). These contain a number of important metabolic enzymes and are an essential part of the cell's structure.

Plant cells typically contain spherical or disk-shaped *plastids*. These may contain the green chlorophyll, being known as chloroplasts, or they may be colorless plastids concerned with the formation of starch or other syntheses. There are other types of colored plastids too, which may be like the pigment spots of certain one-celled or multicellular animals in nature. As plant cells grow older, they become filled

Fig. 56. The Golgi material in a red corpuscle of a frog. Prepared by Golgi's silver impregnation method. (After Sinigaglia, 1910)



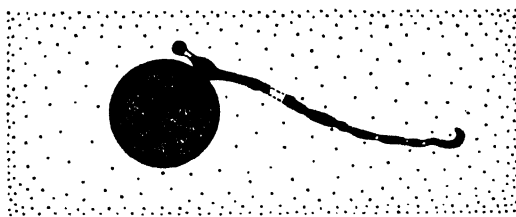


Fig. 57. The close relationship between certain chromosomes and the nucleolus as seen in a microsporocyte of corn, *Zea mays*.

with vacuoles which merge to form one large central vacuole, filled with cell sap. In animal cells too vacuoles may occur, although they never achieve the prominence characteristic of most plant cells.

Found only in animal cells are the so called Golgi bodies, whose structure and function are far less clearly understood than those of the mitochondria (Fig. 56). Still other granules, beyond the limit of visibility with the ordinary microscope, have also been separated from the cell, and these too have been found to contain important biochemical substances. The cytoplasm also contains numerous sorts of granules and droplets of inert food or waste substances, fats and oils, yolk, inorganic crystals, and the like.

Cell Membranes

There are many membranes in the cytoplasm. The nucleus is separated from the cytoplasm by a thin viscous film or membrane much like that which surrounds the entire cell. Like the outer cell membrane this too is protoplasmic and alive. Besides these two membranes there are many others within the cell. Some, like those of the mitochondria, chloroplasts, and the nuclear structures called chromosomes, are more or less "permanent," while others form and dissolve again. Though these may be thought of as forming invisible frameworks throughout the entire protoplasmic mass, some relatively stable and others quite transient, none of them are fixed or rigid structures like a cell wall, but flexible ones produced by the interaction between the molecules of the two parts which they separate.

The Nucleus

This is a more or less spherical, grayish transparent body. The structures within it are not easily observable through the ordinary microscope while the cell is alive, but various techniques of slicing and differential staining reveal them clearly and show that they change during different cellular activities.

The main mass or substance of the nucleus, the nucleoplasm, has the characteristic structure of protoplasm generally, but within this relatively clear ground substance there are a number of very fine crooked threads (Fig. 54) whose nature changes as the cell and its nucleus pass through various phases. These threads, the chromosomes (Gr. *chroma* = color + *soma* = body), are composed of substances collectively termed chromatin, because of their affinity for certain dyes. The chromosomes become shorter and thicker, relatively large and robust structures, during the process of cell division. Chemically, chromatin consists of nucleoproteins, and within these persisting yet changeable structures lie the genes.

Associated with specific chromosomes in the resting nucleus are other nuclear constituents, the nucleoli (Fig. 57). As cell division progresses these nucleoli disappear. Then in the later stages of division they reappear, again in specific regions of certain specific chromosomes. The fate of the nucleolar substance when the nucleolus disappears, and the role of the nucleolus itself, both in the resting and the dividing cell, are still unknown.

MITOSIS

Mitosis in a Hyacinth Root Tip

Chromosomes contain genes, the hereditary determiners, and are distributed from cell generation to cell generation by a precise and intricate mechanism. This is the process called mitosis (Gr. *miton* = thread), so named because of the thread-like shapes assumed by the chromosomes. It is an almost universal method of producing new cells and is therefore fundamental to the process of growth, repro-

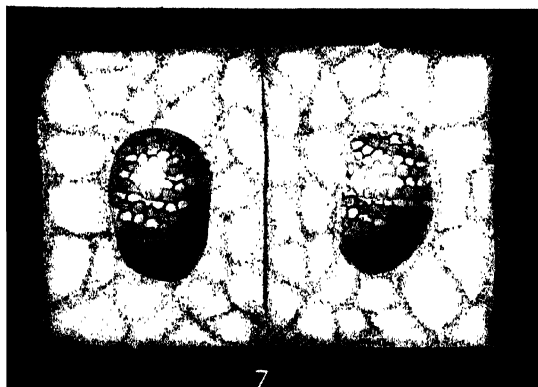
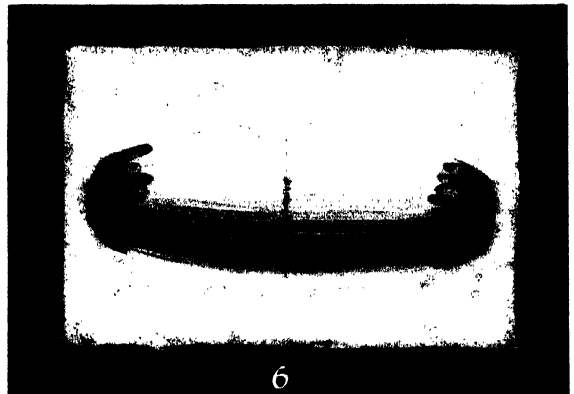
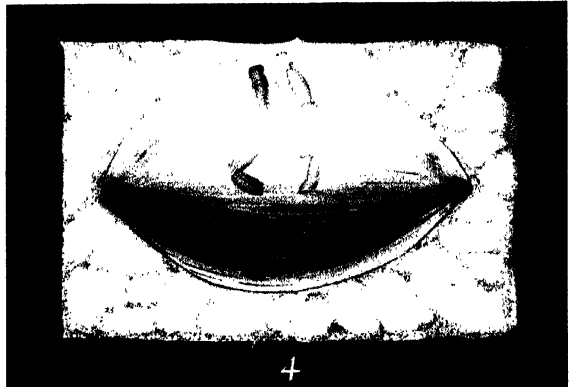
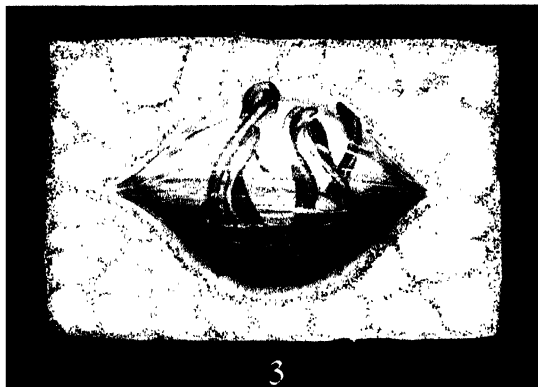
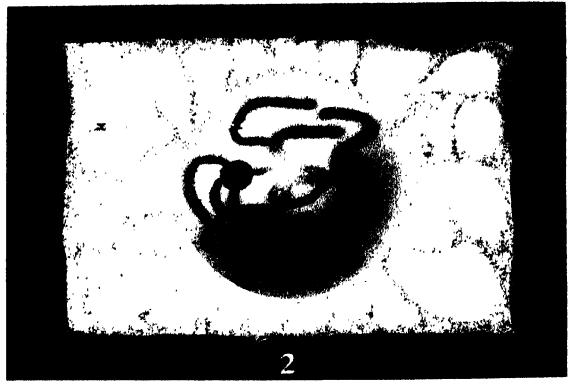
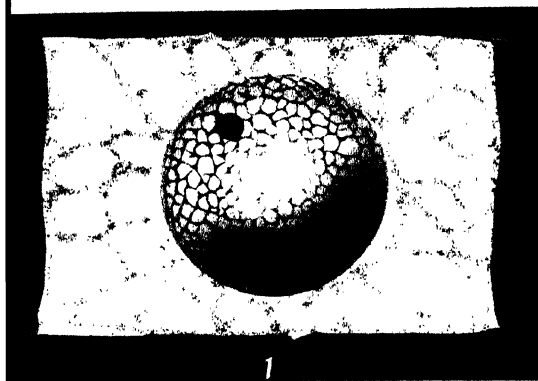


Fig. 58. Mitosis in cells of root tip (semi-diagrammatic). 1. Interphase, chromonemata forming a network, two nucleoli visible. 2. Medium prophase, chromonemata in double ribbons. 3. Late prophase. Chromosomes have formed. Nuclear membrane broken down, and spindle with fibers has formed. 4. Metaphase, chromosome doublets in equatorial plate. 5. Anaphase, chromosome doublets separated, moving toward the poles of the cell. 6. Telophase, chromosomes at poles about to lose visible identity; a new cell wall forming at equatorial plate. 7. Late telophase, chromonemata forming a new network within the reforming nuclear membranes, new cell wall almost completed, two daughter cells formed.

duction, and hereditary continuity by which life is maintained.

The hyacinth root tip is an excellent subject for the study of mitosis because of its rapid growth and delicate structure. Many cells are at all times undergoing mitosis, so that all phases of the process can be seen. An entire root, of course, is far too thick to examine directly, and the cells and their structures are too transparent to be observed in detail. Methods of killing such tissue and of slicing and staining it must be used, and from such cells, caught in mid-change, we may piece together the story of mitosis. Any conclusions drawn from the study of such fixed material may then be checked and modified by observations of living material. Assume, however, that it is possible to watch the living action as one might if he had the power of seeing it directly.

The entire root is made up of thousands of transparent box-like cells, smallest near the tip, and of increasing length and size further from it. It is in the region of the smaller cells that active cell division is going on, and some cells are just about to begin the process while others are at all intermediate stages. The whole dynamic process of mitosis can be divided into four main parts or phases: prophase, metaphase, anaphase and telophase (Fig. 58). At the end and at the beginning, there is an interphase.

Interphase. Between the periods of mitotic division comes what is sometimes misleadingly termed the "resting stage." It is anything but one of rest, however, for while the nucleus no longer shows visible change or activity, the cell embarks upon a period of active metabolism and growth which continues until each of the two new cells is as large as the parent cell which produced them, and sometimes considerably larger.

Prophase. The beginning of mitosis is signaled by increasing visible activity within the nucleus. The chromosomes writhe and twist, and become more conspicuous, since they shorten and become thicker; and it now be-

comes apparent that each thread is actually double. By coiling and by accretion of other nuclear material, these threads become transformed into relatively thick, short, double sets of rods, the chromosomes.

While these changes have been going on, the nuclear membrane has dissolved, so that there is no longer a clear line of demarcation between the nucleoplasm and the cytoplasm. The clearer nuclear region, within which lie the chromosomes, swells and soon changes from its original spherical shape to one more like a short, thick barrel. Because of its shape, this jelly-like, glassy structure is known as the *spindle*.

Metaphase. The double chromosomes, held together at a single undivided point, now become arrayed midway between the two ends of the spindle in a plane — the equatorial plane — which lies at right angles to the spindle axis. This is the metaphase of mitosis. Under certain conditions of stress, chemical treatment, or lighting, thread-like structures called spindle fibers appear within the spindle, attaching the single undivided part of each double chromosome to the two opposite poles of the spindle. Thus, when the attachment point divides, at the close of the metaphase, one member of each chromosome doublet is attached to a fiber from one end of the spindle, and the other member to a fiber from the other end.

Anaphase. Now the two duplicates of each chromosome begin to pull away from each other and to move toward opposite spindle poles, seemingly pulled or guided by the spindle fibers. The distance separating them increases, and soon the chromosomes part company completely and approach opposite poles of the spindle. This period of migration is the anaphase.

Telophase. Though their separate identities remain, the chromosomes now cease to be clearly visible as they swell up and become diffuse, except for the thin central thread at the core of each one. A nuclear membrane forms around each of the two groups of chromosomes,

thus making two nuclei. Across the equatorial plane, a row of granules appears. These coalesce to form a structure, the cell plate, upon which the new cell walls are laid down, dividing the daughter cells from one another. More minute liquid droplets form in this region, thus initiating the ultimate separation of the two cells. The secretion of the new cell walls follows. This is the telophase, or last phase of mitosis.

What Mitosis Achieves

At this point a fundamental question arises. What has been achieved by this process? First mitosis divides the cytoplasm into approximately equal halves, but it duplicates and then divides the nuclear chromatin material with exact equality, both as to quality and quantity. Mitosis thus produces two cells with identical sets of chromosomes. Each daughter cell is the exact counterpart of the mother cell. Also important may be the reduction of the ratio of volume to surface of the cell. As a cell grows without division, its surface increases much less rapidly than its volume, and this change in surface-volume ratio may reduce the relative number of molecules which move in and out of the cell, so that it may not continue to exchange molecules rapidly enough to maintain its life processes at an optimum rate or level. If this is true, then the process of cell division, by keeping down the ratio of volume over surface, may be important to the efficiency of the entire cell.

Functions of the Nucleus

In Reproduction. Our observations have shown that the nucleus plays a most conspicuous part in mitosis. Indeed, most of the process appears to center on the business of distributing nuclear material quite exactly between the two new cells. The nucleus of each cell, as carrier of hereditary characteristics, must be adequate for its major role. In multicellular organisms, including man, mitosis alone is seldom the method of reproducing new individuals, but it produces more cells for increase in body size and for repair and



Fig. 59. Removing the nucleus from an amoeba by the micromanipulator.

replacement of lost or damaged cells. However, some less highly organized multicellular organisms produce new individuals merely by pinching or budding off whole groups of cells which have themselves been produced by mitosis. Though practiced by both plants and animals, this is known as the *vegetative* method of reproduction, as distinct from reproduction by special reproductive cells such as sex cells. But even in sexual reproduction the new cells are produced by a modification of the nuclear mechanism found in mitosis. This, and related matters, will be considered in more detail in Chapter 24.

In Maintaining Life. The removal of the nucleus and the chromatic material from a cell has profound effects upon it. Nuclei have been removed from protozoa by various methods. Robert Chambers and others, by means of the micromanipulator, have removed the nucleus from an amoeba (Fig. 59) apparently without inflicting immediate damage on the animal. The nucleus can be plucked out through the cell membrane, which closes



Fig. 60. Pairing between corresponding chromosomes is best seen in the giant salivary gland chromosomes of flies, such as *Chironomus*, a midge. If both parents are of the same strain, pairing is almost perfect. When the parents come from strains that have somewhat different arrangements of genes, pairing is imperfect, as here; only parts of the chromosomes with identical patterns of bands can pair intimately. The bands are thought to contain the genes.

over the wound without a trace. The enucleated amoeba more or less normally continues its activities for some time, but seems to lose its ability to grow and repair itself. It shrinks in size, and within twenty-four hours succumbs to the operation. From this and similar experiments it appears that the nucleus is essential to the life of the cell.

In Controlling Development. Large multicellular organisms arise from but a single microscopic cell, the egg; and the egg must generally first be fertilized by an even smaller male cell, the sperm. Both these cells bear chromosomes which endow the resulting organism with the genes that control the production of features inherited from both parents.

The genes, local parts of the threadlike chromosomes, are the real units of heredity. All cells produced from previous cells by mitosis normally contain replicas of the original chromosomes and genes, and there is direct visual evidence that chromosomes maintain their identity and individual form from generation to generation. In certain rather unusual cases, as in the cells of the salivary glands of the fruit fly *Drosophila*, the chromosomes become enormously enlarged. Because of their size, these are exceptionally good subjects for study, and they reveal a characteristic banded or cross-striated structure which is handed on in the same precise, individual pattern from generation to generation (Fig. 60). It is now thought that these bands contain the indi-

vidual genes, or perhaps a number of genes apiece. Experimental evidence has shown that when certain regions of chromosomes are damaged or missing, characteristic defects occur in the organism. Briefly, it is known that genes, individually and collectively, determine what synthetic processes a cell can perform. But it is also known that the chemical processes of a living organism are controlled by organic catalysts, that is, enzymes (see page 62). In other words, the genes are not to be thought of as being themselves the usual hereditary characteristics, but forerunners of enzymes or possibly themselves the ultimate enzymes that initiate such processes within the cell so as to produce certain characteristics under particular conditions. In addition to this function, genes also have the significant power of duplicating themselves, that is, they can catalyze their own synthesis. They are thus autocatalytic or autotrophic, in addition to sponsoring other specific reactions of development and metabolism.

The Forces Involved in Mitosis

The microscopic changes that occur in a cell during mitosis can be seen, but attempts at untangling the web of chemical and physical events that underlie them have not yet been signally successful. It is quite clear that the observable changes can be but crude expressions of the invisible molecular processes that constitute the real events.

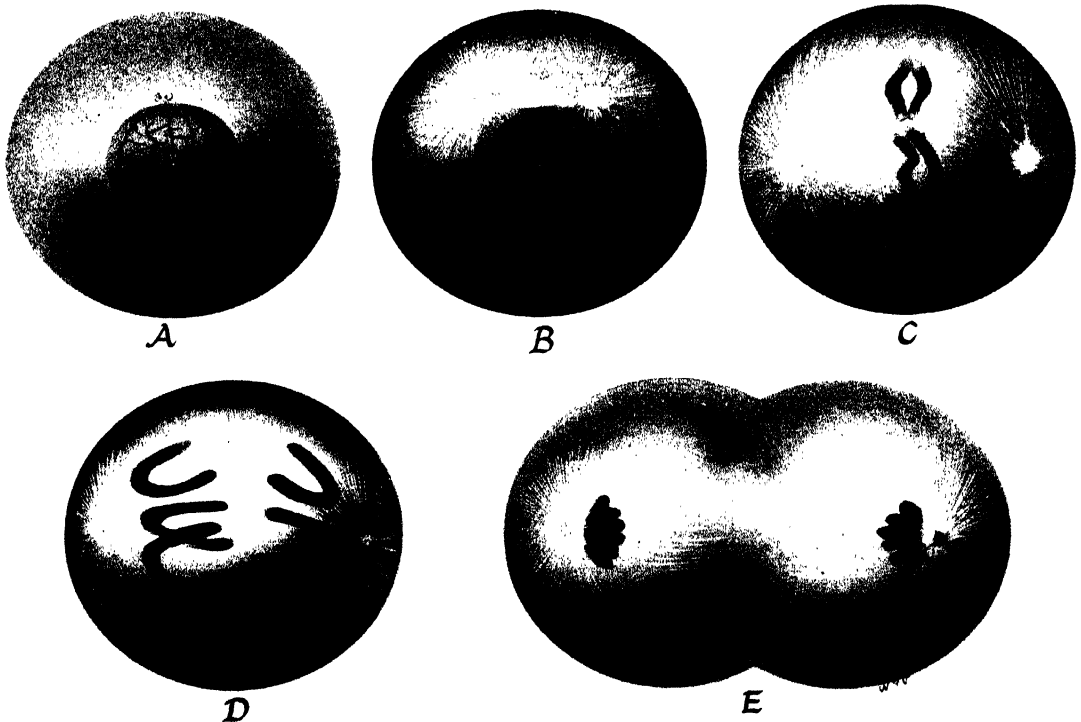
The duplication of the chromosomes is evidence of autosynthesis. The disappearance of the nucleolus and increase in mass of the chromosomes is indicative of some transfer of materials. Changes in surface tension help to re-form and re-shape protoplasmic structures to meet new stresses. The dissolution of the nuclear membrane and the formation of the spindle reveal that changes of colloidal phases and sol-gel transformations are occurring. In mitosis it is easy to observe the appearance of the spindle, the spindle fibers, and the chromosomes, and to note the arranging of the chromosome doublets on the equatorial plate, followed by their subsequent migration to the spindle poles. But it is far from easy to determine the exact forces and chemical processes that achieve these results, and at present no explanation can be considered even nearly complete or final.

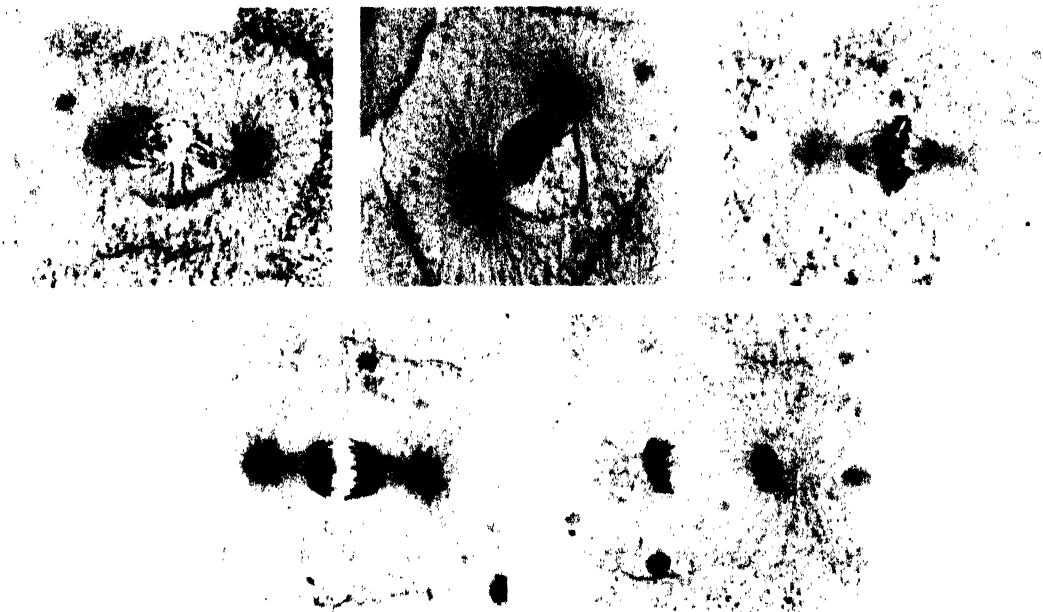
The Spindle. The spindle is primarily of nuclear origin, although in some cells the cytoplasm may contribute to its formation. The spindle is a relatively tough, elastic, and clear

mass of protoplasm that can be moved about bodily by the dissecting needle of a micro-manipulator. It can even be fished out of a cell, and it withstands considerable twisting and stretching without permanently losing its form or consistency. Spindle fibers are not usually visible in the spindle of a living cell, but appear under the abnormal conditions of chemical fixation, pulling, or stretching. In many animal cells, fibers are formed in the cytoplasm that radiate like a star in all directions from the spindle apex or centrosome (Fig. 61). These are the asters (Gr. *aster* = star), and the astral rays forming them are channels of a relatively liquid cytoplasm rather than fibers. The puzzling spindle fibers, too, may be channels, or indications of an orientation of molecules lengthwise through the spindle, from equator to poles (Fig. 63).

Chromosomes isolated from the spindle nevertheless separate slightly — a fact which implies that the separation is somehow initiated by the chromosomes themselves and not by an outside agent. The aid of the spindle

Fig. 61. Mitosis in an animal cell (whitefish). *A* and *B*. Prophase. *C*. Metaphase. *D*. Anaphase. *E*. Telophase. Note the asters in *C* and *D*. These figures are of course diagrammatic.





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Fig. 62. These are photographs of essentially the same mitotic stages as those shown in Fig. 61 (whitefish). Top: Prophase, later prophase, metaphase. Bottom: Anaphase, telophase

fibers is somehow involved in their further movement. In at least some cells (*Tradescantia*) the elongation of the central spindle region helps by pushing the initially separated chromosomes apart.

Formation of the Spindle. Even less is known about the formation of the spindle and its rays or fibers than about the movement of the chromosomes. Many attempts have been made to duplicate some of the forms and structures of the mitotic cell by an interplay of known forces, in the hope that these might throw some light on the forces active within the cell. Though none of these have resulted in any very conclusive answers, they cannot be dismissed as worthless. It is suggestive that figures showing superficial resemblance to mitotic spindles have been produced in various ways, always by opposing two centers of force, thus creating a tension or distortion in an otherwise uniform substrate. Thus two radiating gradients of salt concentration cause suspended carbon particles to arrange themselves in the form of a spindle with astral rays

and a structure like an equatorial plate. Magnetic lines of force produced with a magnet and iron filings, stresses in plastic materials as seen under polarized light, or even simply a rubber membrane grasped at two points with the fingers and stretched, will produce patterns roughly simulating spindles. Though these devices yield no answer, they demonstrate that opposing fields of force can produce relatively complicated structures, superficially similar to the mitotic figures. The mechanism of mitosis may some day be explained in terms of the interplay of such forces.

The Nature and Function of Genes

Catalysis. Practically all chemical reactions in a cell occur under the sponsorship of specific enzymes, and enzymes are proteins, or at least have basic protein components. Genes also are protein in nature, and so it has long been suggested that genes must have some close relation to enzymes. This suggestion has recently been strengthened by work with

the so-called "biochemical mutants" of the mold *Neurospora*. It seems quite clear that particular genes determine the presence of the specific enzymes essential for individual chemical steps of metabolic processes.

Autosynthesis. Since reproduction, or self-duplication, is one of the most characteristic features of a living organism, the problem of the duplication of the genes strikes at the very root of the problem of life.

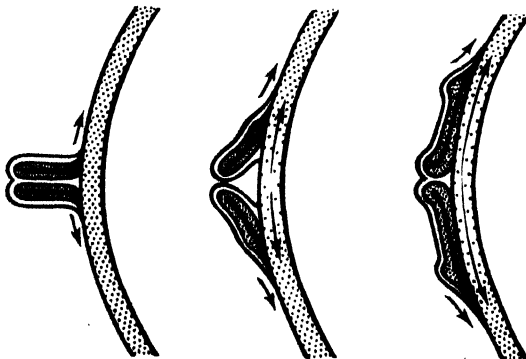
Little is known about how this takes place. At best it can only be said that certain forces within the gene molecules enable them to arrange available chemical substances into the same structural pattern which the genes themselves possess. It may be the same power which enables a gene in one chromosome to attract its counterpart in another, a phenomenon which occurs during a phase in the production of gametes, called synapsis. The chemist and the physicist still have much to do before synapsis and autosynthesis are explained in terms of chemical affinity and the forces within the nucleus of the atom. Genes are remarkable for their continuing stability through countless generations, yet no less remarkable for their unique ability to undergo structural changes which alter their effect on metabolism without destroying their auto-synthetic power. Upon this property rests ultimately the whole structure of evolution and hence of varied life on earth. Such changes in structure and effect, called *mutations*, are

relatively infrequent, perhaps not more than one gene in 100,000 mutating in a generation; yet mutations are far from unusual because there are so many genes in any cell, and so many individuals in any population. Together with the inherent stability of the genes, mutations form the very foundation of evolution.

Mutations occur apparently independently within the single genes. The direction of mutation appears to be quite unpredictable, although a given gene may display a greater tendency to change in one way than another. As might be expected, mutations may be produced by environmental factors. Increase in temperature may cause an increase in the rate at which they occur. A far more effective cause is the penetrating radiations of radioactive substances and X-rays. No matter by what means they are induced, most mutations are apparently blind and random. Many seem to have no particular effect on the organism, but most mutations, because they are likely to produce a variation which disturbs the delicate balance between the organism and its environment, tend to be harmful.

Changes in the effect of genes may also be brought about by rearranging the sequence of genes within a chromosome. This indicates that no gene is sufficient unto itself, but always functions as a subordinate unit of the entire complex. The way in which these random changes form the raw material upon which the forces of evolution act will be discussed in Chapter 24.

Fig. 63. Belar's hypothesis of the relationship between separating pair of chromosomes and spindle fiber



Differentiation of Cells

If a multicellular organism, such as man, is produced from a single cell by mitosis, then each cell of which the organism is composed has perfect replicas of the chromosomes, and hence the genes, of the original fertilized egg. The question then arises: if genes determine what a cell will do and what it will be like, why are not all cells in a complex organism exactly alike, and why do they not all perform the same function? A brief reconsideration of the nature of the gene and of cell division, will answer this question.

Genes produce enzymes, or are themselves enzymes, which direct the cell to do certain things under certain conditions. Uneven distribution of food matter or other substances in the cytoplasm within the original fertilized egg will produce cells with varying amounts of such substances. Because of the original gradient of food distribution in the egg, the genes within the various cells of the embryo will not all have the same cytoplasmic environment within which to express their potentialities, even though these genic complements of all cells are identical. Much more, then, will the cells of the skin, for example, have different environmental conditions than those lining the stomach. Moreover, the environments of these two types of cell are different from those of early embryonic days. Hence it is not surprising that they do not look and behave in the same way (Fig. 64).

FROM INORGANIC TO ORGANIC

Genes and the Cell

In view of the complexity of the living cell, it is scarcely conceivable that life first appeared as a complete cellular organism or even as a single cell. Even a single chromosome

is so complex that it can hardly have sprung suddenly into existence as a result of a favorable confluence of forces and matter. Fortunately we now have knowledge which contributes toward at least a partial answer of this fundamental question. We know that matter, both living and non-living, did not always have the form it has today. Somewhere and somehow the first ancestor, or ancestors, of all the organisms on earth must have originated. Cells always come from pre-existing cells, and yet there must have been a time when cells as we know them did not exist. How then did the first ones come to be?

The fact that some cells are relatively simple, whereas others appear to be more complex, suggests that the more complex ones may have arisen in some manner from the simpler ones, for vast stores of evidence attest that nature operates in this manner.

Nucleated cells do not represent the beginning of vital organization. The minute blue-green algae, the Cyanophyceae, do not always have a well developed nucleus, although they generally contain an area which is nuclear in nature since it contains scattered chromatin which produces chromosomal struc-

Fig. 64. Specialized cells found in a multicellular organism. Each has the same kind of chromosomes, and hence the same genic components. Top: Squamous epithelial cells lining cheek; ciliated columnar epithelial cells in trachea; smooth muscle cells; multinuclear striated muscle cells of skeletal muscle; white blood cells. Bottom: Cartilage cells, end of rib; bone cells in calcified matrix; loose connective tissue under skin; nerve cells or neurons; fatty tissue cells.



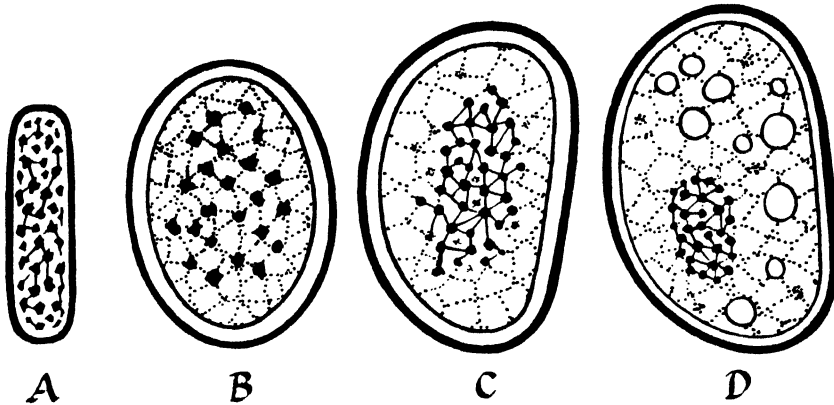


Fig. 65. Simple organisms with chromidial nuclei. The dark particles represent chromatin. *A*. Typical bacterium with chromatin scattered throughout its entire cell. *B*, *C*, and *D*. Different species of blue-green algae showing intermediate conditions between the distributed and the delimited type of nucleus.

tures divided between the daughter cells in mitotic fashion. Yet some Cyanophyceae show no sign of even this nuclear area, but have their chromatin scattered throughout the entire cell. This is probably not just an idiosyncrasy of this particular organism, since the same diffuse nuclear structure appears to be general in certain organisms regarded as being on a still lower level of organization, namely, the bacteria (Fig. 65). In view of these gradations of nuclear structure it is almost impossible to avoid the impression that we are here dealing with an evolutionary sequence. We might perhaps consider the bacteria as free-living nuclei or even single chromosomes, a condition which they would share with the lower algae. The more advanced members of the latter group might be considered as representing stages in the gradual development of an organized mass of cytoplasm around the nucleus—that is, a cell body.

The Filterable Viruses

But the process of tracing organisms back to ever simpler ancestors must end somewhere, and that will be the dividing line between the living and the non-living. Far beyond the range of the ordinary microscope but within the range of the electron microscope are minute bodies called filterable

viruses, so called because they are small enough to pass through the pores of a fine porcelain filter.

There is still considerable controversy over the nature of these disease producers, which appear to be on the borderline between the animate and the inanimate. The main controversy stems from the fact that they seem to have all the essential properties of living organisms when placed in their natural environment, which is the protoplasm of their proper host. They reproduce; that is, they are capable of synthesizing the substances of which they are composed and thus of producing more of themselves. Chemically they are nucleoproteins, and thus of the same nature as genes. They are even capable of heritable changes or mutations. However, they possess one characteristic in particular that is most unlifelike and hence most disconcerting to those who would classify them. In 1935 an American chemist, W. M. Stanley, isolated in the form of needle-like crystals the virus that causes the tobacco mosaic disease, and it was found that these crystals may be stored in a bottle on the laboratory shelf for an indefinite time without showing any sign of activity.¹ This resemblance to an inanimate chemical substance appears to be most unorthodox for a living

¹ This great discovery won Stanley a share in the Nobel Prize award for Chemistry in 1946.

organism. In addition, crystallization is accepted by the chemist as an approach to chemical purity, and no living organism has been conceived of as a single chemical substance. Yet these crystals are unmistakably the virus itself. For, injected into a tobacco plant, they resume their life-like activities. Thus they pass, so to speak, from a living to a non-living condition and back again, depending on circumstances. No other organisms are capable of such a feat. Only bacteria and the spermatozoa of a few species approach such behavior, and these only if they have been rapidly frozen and then carefully thawed out. Nothing is commoner knowledge than that the passage of life to death is generally a one-way road.

From Non-Living to Living

The "Dividing Line." The distinction between living and non-living is perhaps merely verbal: are the viruses alive, or should they be called inanimate autocatalytic agents? Any such argument would appear tantamount to arguing where to draw a line between black and gray. While it is now thought probable that the viruses are an extreme case of parasitic specialization — forms which have degenerated from once whole cells — their existence may be taken to suggest that life was the outcome of an evolutionary process which began with structures something like them.

Perhaps, to speculate further, these free-living organic molecules represented solitary genes, in which event the sequence would be, first, free-living genes, as represented by the virus-like molecules; then, by mutations, increasing efficiency through increased complexity, producing a string of genes, a chromosome, as represented by certain bacterial forms; then, by similar evolutionary processes, unprotected nuclei, as represented by other bacteria and by some of the simpler types of blue-green algae; next the gradual acquisition of cytoplasm and cell structure, as exemplified by other members of this group; and finally, the fully developed cell, with a well-defined nucleus, cytoplasm, and a cell membrane.

Formation of Organic Compounds

This sequence, even if it is the way things actually happened, by no means solves the problem of the origin of life. Among other writers, the Russian chemist Oparin, in his book *Origin of Life*, has proposed ingenious hypotheses to answer such questions. How, we may ask, could virus-like units that depend for their existence on pre-existing organic compounds be considered similar to the first form of life? In order to answer this, it is necessary to recall that as the crust of the new-formed earth cooled, there was a steady process of compound formation, resulting from forces inherent in the structure of the atom.

Spectroscopic examination of stars in various phases of evolution shows the presence of hydrocarbons — simple organic compounds consisting only of hydrogen and carbon, such as CH (methane) — on the cooler stars. From this and other facts, it may be concluded that such compounds must have appeared very early in the cooling of the earth. Present also under such conditions are carbon in its molecular form (C_2) and molecules of carbon united with nitrogen, forming CN (cyanogen). Fairly complex hydrocarbons have also been found in meteorites, thus further supporting the assumption of their abiotic (non-living) origin. In all cases, carbon appears either as an element or bound to nitrogen or hydrogen. Carbon dioxide, essential to modern plants, appears to be of secondary origin. The free hydrogen, nitrogen, and oxygen that were a part of the primordial sun-mass which formed the earth must have largely escaped into space, for the gravitational pull of the earth would have been insufficient to hold these lighter elements at the temperatures then existing. These gases, which form such a large proportion of our atmosphere today, must have been chemically combined with heavier atoms, later to be released. Inert light elements could not have been so held, and indeed such inert elements as helium and neon are present in the earth's atmosphere only as traces.

All the water of the earth was quite certainly

in the form of superheated water vapor, or steam. When carbon compounds containing metals — called carbides — come in contact with water vapor, hydrocarbons are formed. Similarly, at high temperatures metals unite readily with nitrogen to form nitrides, and in contact with superheated water vapor, these produce ammonia, as do various similar reactions. These two compounds — the hydrocarbons and ammonia — contain the three most essential elements found in living organisms: carbon, hydrogen, and nitrogen.

Hydrocarbons form the basis of a great many potential oxidation products, giving rise to such organic compounds as alcohols, aldehydes, and organic acids and thus introducing oxygen, the fourth basic element in the organic compounds of living organisms. The hydrocarbons and their derivatives have enormous chemical potentialities. Methyl alcohol (C_2H_5OH) can be transformed into formaldehyde (CH_2O) by the removal of hydrogen, and six molecules of formaldehyde may be changed into one molecule of a simple sugar, glucose ($C_6H_{12}O_6$). This can happen spontaneously in the presence of light, or more rapidly under the sponsorship of a suitable catalyst. Furthermore, reactions of hydrocarbon derivatives with inorganic nitrogenous compounds — by standing, or under light — can give rise to organic nitrogenous compounds with the properties of simple proteins, compounds essential to life. Thus formaldehyde (CH_2O) may condense to form glycolaldehyde ($CH_2OH \cdot CHO$), which by oxidation-reduction processes produces the compounds glycol ($CH_2OH \cdot CH_2OH$) and glycolic acid ($CH_2OH \cdot COOH$). The latter, reacting with ammonia (NH_3), produces glycine ($CH_2NH_2 \cdot COOH$), the simplest amino acid and the building stone of the proteins.

It can thus be shown that the formation of complex organic compounds, including even the proteins, could occur quite spontaneously under conditions which probably existed on the earth shortly after its inception.

Evolutionary Tendencies in Compounds

Such compounds, existing in the form of

complex mixtures, show a number of peculiar tendencies of an evolutionary nature. They tend to form increasingly long chains of molecules, thus producing not only more complex molecules, but a greater variety as well. Such giant molecules may form colloidal solutions in water, and by virtue of certain radicals (NH and OH) may marshal water molecules about themselves in an orderly manner, thus in effect surrounding themselves with a film and isolating one colloidal particle from another, while the cohesive forces of the water at the same time tend to hold them together. Such colloids are said to be "water-loving" or hydrophil colloids. In this manner a semi-solid, semi-liquid system might come about similar in chemical composition and physical structure to protoplasm.

Competition and Survival

In consequence of these and similar activities, a multitude of the most varied organic compounds must have been formed long before the appearance of the first organic complex which could have been called alive. Moreover, it would seem that conditions necessary for the creation of life could have existed only on a completely sterile and lifeless world; for only then could a gradual accretion of organic molecules have existed long enough to attain a complexity and efficiency approaching that of a simple living unit. Such inanimate evolution of organic compounds could not well take place on the earth today, for intensely competitive life is everywhere quick to use for its own metabolic purposes any stray organic molecule that becomes available. Incubation of life on earth probably demanded a sterile crucible at the outset.

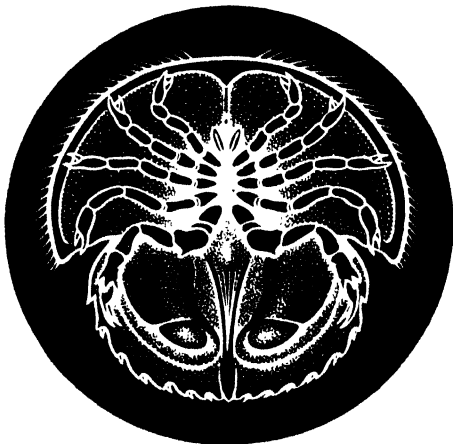
Competition among the first autotrophic complexes must have been keen indeed, and only the most efficient ones could have survived as the original supply of abiotic organic compounds dwindled. They could have survived in several possible ways. An organism could evolve a mechanism enabling it to use other sources of energy than those bound within organic compounds, such as light, thus

enabling it to tap the vast stores of inorganic compounds for its raw materials; or it could evolve a mechanism for attacking the substance of other living organisms. It is likely that light was first used by organisms to accelerate the reactions involved in their use of organic compounds, and that the enormously significant process of photosynthesis developed later. The use of light was in itself nothing new, for light was probably the main source of energy in the synthesis of the original abiotic organic compounds, but it was probably then used with far lower efficiency than it came to be later.

Thus the first living organism may have been rather like a complex molecule, such as a virus. The fact that all known viruses depend upon an available source of complex proteins does not necessarily represent an insoluble problem, since the first living units probably depended on similar sources of structural materials and energy. The gulf between the living and the inanimate appears to be slowly but surely narrowing as knowledge increases. The story of the genesis and evolution of life appears to have been roughed out; yet the amount of detail that remains to be filled in is almost incalculable.

PART THREE

THE PRINCIPLE OF EVOLUTION





Much of the evidence for the theory of evolution is provided by fossilized remnants of once living things. Above is a group of dinosaur's eggs, perhaps 150 million years old.



The Theory of Evolution

BACKGROUNDS

The Pattern of Life

With minor exceptions, every portion of the earth's surface teems with life in the greatest variety of forms and habits. Every creature, however fragile, gives evidence, by its very survival, of qualifications that fit it for its environment. Yet, in spite of diversity of form, size, and activity, there is a striking recurrence of design. Life is not a formless jumble. Group similarities emerge that are visible even to the untrained eye. We automatically differentiate between animals and plants. We distinguish groups with obvious characteristics in common, such as the internal articulated skeleton of the vertebrates. Within these groups we recognize other fraternities, such as the animals that have hair and are warm to the touch, like the mammals. As the groups become smaller, we see an increasing community of characteristics.

Despite the diversity of forms, there is an amazing harmony between the individual and its environment, and the group to which it belongs does not seem to determine its choice of environment. Thus whales are at home in the open ocean, moles burrow underground, and bats fly. Yet all are mammals and have a fundamental similarity in structure, and each fits as perfectly into its environment as the cake fits the mold in which it was baked. Lest this generalization suggest too simple a solution, remember that the ocean also harbors the jellyfish; that earthworms also burrow, and dragonflies also fly. Despite all this perfection of adaptability, no individual adjustment to a particular environment appears to be the only one possible. Moreover, every creature represents a part of the environment of certain

others. None lives independently, and usually the lives of many are closely interrelated.

This does not imply that every creature was designed for a special purpose, or that each was created so that another might live. The human mind being what it is, the conclusion that every living creature must in some way benefit man is tempting, but it is not very sound in the face of the evidence. For as man uses other creatures to further his interests, so others use him for theirs, and in neither case does the taker consult the wishes of the donor. The mosquito sucks human blood, the malarial parasite lives in the human bloodstream, and the sheep and the cow die to still man's appetite. If any of these organisms were to disappear, life would still continue. Nor, if man were to become extinct tomorrow, would life cease; perhaps it would continue more peacefully than before. The removal of one creature will not disrupt the web of life, though it will alter its pattern slightly. Many creatures that have lived in the past have become extinct, and others have replaced them in their roles in nature.

The Theory of Evolution

If the interrelationship of organisms does not argue that each one was made for another, the question remains: How account for the fact that in the diversity of living creatures each appears to fit into a niche especially designed for it?

In the light of present evidence, it is not likely that each creature was designed and produced by a single act of creation. Since each is related to the existence of others, that very interdependence might be considered the reason for their diversity. The fact that many which lived in the past were different from

those of today could then be explained only on the ground of repeated acts of creation — and destruction. The only answer that has been found to fit the observed facts, and to satisfy the logical mind, is the theory of evolution. This theory can be expressed with the greatest simplicity: The specialized creatures of today have descended by gradual change from different and usually simpler creatures of the past. Of course, this statement offers no explanation of how or why such a thing should happen, but merely affirms that it did. The fact that we do not completely understand how a chick develops from an egg does not make the process imaginary. Likewise, the fact that we do not know how or why simpler creatures of the past evolved into the more complex ones of today does not alter the situation.

History of the Theory

The Ancients. As early as 450 B.C. the Greek philosopher Empedocles conceived a crude idea of evolution not unlike the modern concept. He viewed "nature's cauldron" as producing, through indiscriminate mixing of its elements, heads without arms, arms without shoulders, and other impossible formations. As these parts met and united by chance, he visualized the production of horned heads on human bodies, oxen with human hands, and many other monstrous forms. Most of these, according to Empedocles, disappeared as suddenly as they arose, being unfit to live; and only rarely, when several parts were adapted to each other, could the creation persist. In the light of modern knowledge, this theory is crude, but in a modified way, and less grossly than here stated, it describes the principle of natural selection. Aristotle over 2000 years ago said that "Nature makes so gradual a transition from the inanimate to the animate kingdom that the boundary lines which separate them are indistinct and doubtful." Whatever he may have meant by it, the truth of the statement becomes increasingly apparent as knowledge increases. The idea that nature operates by slow change occurred to many

minds down the ages, sometimes intuitively and sometimes as the result of considered reasoning.

Early Modern Theorists. The first important modern writer on the subject was George Louis Leclerc de Buffon (1707-1788), who presented a theory of the direct modification of animals by external conditions. A contemporary, Pierre Louis Moreau de Maupertuis, framed a theory of organic evolution based upon mutation, natural selection, and geographic isolation — a theory which foreshadowed much that is held true today. Erasmus Darwin (1731-1802), grandfather of the illustrious Charles, advanced the idea that all animals alike have been produced from a similar living filament. He explained this by suggesting that the first living filament was endowed with animality and with the power of acquiring new parts which bestowed upon it new propensities that were directed by environmental factors. The French biologist Lamarck (1744-1829) presented the world with the first widely known, logical theory of evolution. We do not accept his explanation today because we have access to enormously greater knowledge, but his theory of the inheritance of cumulative modifications induced by the action of the environment fitted in well enough with the facts at his disposal. Herbert Spencer (1820-1903), primarily a philosopher but also a competent biologist, preached a full-grown doctrine of evolution in the years immediately preceding the publication of that scientific bombshell, Charles Darwin's *Origin of Species*. Spencer was a pioneer in this line of thought, for few naturalists of his time shared his views.

Darwin and the Theory of Natural Selection

His Debt to Malthus. We have it from Charles Darwin himself that Robert Malthus (1766-1834) was the man to whom he was indebted for the central idea of his work. The writings of Malthus had a similar effect upon Alfred Russel Wallace, who in 1858 sent a manuscript to Darwin propounding essentially the same conclusions as those which Darwin had reached as a result of his long study. One-



Fig. 66. Charles Darwin.

time curate of Albury in Surrey, Malthus was also an able economist, and in 1798 published his *Essay on Population*. In this work he argued that the human race always tends to outrun its means of subsistence and that it can be kept in bounds only by the positive checks of famine, pestilence, and war. Added to this he allowed a so-called "moral restraint," but this served, he thought, merely to soften or postpone the working of the positive checks. Darwin read this essay in October, 1838, and the phrase "struggle for existence" profoundly affected him. He wrote, "It at once struck me that under these circumstances favourable variations would tend to be preserved and unfavourable ones destroyed. The result of this would be the formation of new species. Here then I had a theory by which to work."

Darwin and Wallace. Through the recommendation of a friend, Darwin in 1831 had obtained an appointment as naturalist to join a scientific expedition on H.M.S. *Beagle* to sail round the world. This trip, which lasted over four years, gave Darwin much of the

stimulation that later resulted in the formulation of his theory. A patient and methodical man, he worked on his material for twenty years before he considered it ready for publication. It would probably have been delayed still longer if in 1858 he had not received the aforementioned manuscript from Wallace, then in the Moluccas, who asked for Darwin's opinion. Darwin was startled to see that this manuscript contained a complete statement of his own theory of natural selection. He solved his dilemma, with the aid of his friends, in a manner that stands as a classic of scientific co-operation. A joint communication under the names of Darwin and Wallace was sent to the Linnean Society and was read there on July 1, 1858. In 1859 Darwin published his own great work, *On the Origin of Species by Means of Natural Selection*. The tremendous interest in the ideas it presented is evident from the fact that the entire edition was sold out on the day of issue. The storm of controversy started by his revolutionary doctrine may be partly explained when we remember that even in the middle years of the nineteenth century some learned men still seriously contended that fossils, since they appeared to contradict the story of the creation as told in Genesis, must have been hidden in the ground by the devil in order to mislead mankind. We must not forget, either, that in the middle twenties of our own century a school teacher in the United States was accused and convicted of the "crime" of teaching evolution!

Darwin's Theory. Darwin, in short, was not the first man to state the theory of evolution, but his name is indissolubly linked with the concept because his book presented not arm-chair speculation or hasty assumption but carefully gathered evidence, shaped by a combined inductive and deductive method that had not before been applied to this field.

Starting with generalizations based on observed facts, he framed the deductions which explained the evolutionary process. The first generalization was that all organisms tend to increase in geometric ratio. The second was the apparent contradiction that despite this

tendency to increase, population numbers tend to remain more or less constant. From these two points he deduced the struggle for existence. Another fact, hereditary variation, added to the first deduction, led to a second, natural selection. The whole theory could be stated thus: Since organisms reproduce at a rate much greater than that necessary for replacement without, however, visibly increasing in numbers, their numbers must be kept in check by a struggle for existence; and since there is always a great deal of hereditary variation among the individuals in a group, this struggle for existence must have a selective effect in removing the unfit. Thus Darwin proposed that nature works by the empirical method of trial and error; that out of countless trials a few will succeed and will establish themselves in a new and greater harmony with their environment. This is the theory of evolution through natural selection.

That Darwin was a cautious man is evident from the fact that he withheld the publication of his views for the twenty years during which they matured. That he was an honest man is evident from his statement that "I have steadily endeavoured to keep my mind free so as to give up any hypothesis however much beloved (and I can not resist from forming one on every subject) as soon as facts are shown to be opposed to it." Darwin the man, as well as his contribution to knowledge, is surely worthy of our deep respect.

Evidences for Evolution

Since Darwin's day vast stores of additional evidence supporting the theory of evolution have been accumulated, drawn from many fields of biological research. The evidences for the theory are of seven main kinds, from various branches of biological science:

1. *Paleontology* (Gr., *palaio* = old + *onta* = existing things + *logos* = word, discourse) — the science dealing with the life of past geological periods through a study of fossils.
2. *Mutations* — the sudden alterations of

the genes which determine the inherited characteristics of the species of organisms.

3. *Taxonomy* (Gr., *taxis* = arrangement + *nomos* = law) — the classification of organisms according to their natural relationships.

4. *Embryology* (Gr., *en* = in + *bryein* = to swell) — the study of the beginning or undeveloped stage of living organisms.

5. *Comparative Anatomy* — the anatomical comparison of existing organisms.

6. *Comparative Physiology* — comparison of the processes of living organisms.

7. *Domestication* — the consideration of the changes wrought in living organisms, both plants and animals as a result of domestication.

EVIDENCE FROM PALEONTOLOGY

Fossil Remains

In many places on the earth's surface, imprints and formations may be found which are readily recognizable as remnants or impressions of animals and plants. These remains, called fossils (L., *fossilis*, from *fodere* = to dig), known for thousands of years, show that many

Fig. 67. A small fossil eurypterid (sea scorpion). Some reached a length of ten feet.



creatures that lived in the past were unlike any still living today, and that most creatures of the distant past were structurally simpler.

Fossil remains are found principally in sedimentary rock formed by the slow deposit of sand, silt, or gravel on the bottom of rivers, lakes, or seas, or as aggregates of varying coarseness deposited through wave action along the shores of ancient continents (Figs. 67, 68). Fossils occur most frequently in sedimentary rock because the skeletal remains of dead creatures are embedded and preserved in the gradual accumulation. In igneous rock (L. *ignis* = fire), which was molten and flowing before it solidified, or in metamorphic rock, which has been changed (metamorphosed) by heat and pressure from its original form, the fragile structures of living things could not be recognizably preserved.¹ Sedimentary rock is composed of clearly defined strata or layers, and thus shows the succession in time of the various deposits. Observation of sedimentary deposits still in process of creation gives some evidence of the conditions under which ancient fossil-bearing strata may have been laid down and of the length of time required for the process.

Although the rate of sedimentation is greatly influenced by local conditions, it has been roughly estimated that the average rate is about one foot in 1000 years, or even less. The greatest total thickness of sedimentary rock is estimated at about seventy miles, and the ratio of seventy miles to 1000 feet gives some idea of the time involved. More important is the fact that the relative age of a fossil may be determined by the succession of the strata, wherever they are undisturbed, for of course the deeper strata were laid down before the more superficial strata could be deposited on top of them. Even if we cannot say with exactitude how old a fossil deposit is in years, we can say with considerable certainty that one deposit is older or younger than another, and roughly how much.

¹ See Chapter 1, page 18, where the fiery origin of the earth is described.



Fig. 68. Fossils of trilobites, whose close relative, the king crab, survives today.

A method of measuring geological time far more accurately and reliably than by the estimation of sedimentation rates, and one which has yielded valuable information, is based upon the radioactivity of certain elements, especially uranium.² Many such observations have yielded data which make it possible to estimate the age of the earth's crust and of some of the fossils embedded in it. It has been conservatively estimated that the oldest granites are very nearly two billion years old. These are igneous rocks and of course antedate any sedimentary formations.

But the problem of interpreting fossil remains is not quite so simple as all this might

² The rate of radioactive disintegration is perfectly uniform. Since we know the nature of the original substance as well as the end products of its disintegration, and since we know the rate of this process, a comparison between the amount of the original substance and the amount of the end product will show how long ago the process began in any given instance. This requires, of course, that all end products are still present.

imply. As the layers of sedimentary rock are being built up, two opposite processes are also taking place. The surface of the earth is slowly though constantly rising or falling. Regions submerged under shallow seas and in deltas may be lifted by shifting forces in the earth's crust and interior until they become mountain tops. When this occurs, the horizontal layers of sedimentary rock are heaved up, folded, and broken so that discontinuous layers may arise, separated by one or more sharp breaks called *faults*. The result of this process is that while one part of a deposit may remain submerged and protected, another may rise hundreds of feet above it.

With the earth's crust thus changed, the second process comes into play. This is *erosion*, the gradual wearing away of the surface. Flowing and seeping water, a potent solvent, carries with it much of the earth's crust in solution, on its journey to the sea. The violent bursting action of freezing water, as it expands, breaks large rocks and increases the surface exposed to further erosion. The baking heat of the sun causes cracking stresses in the expanding rock. Sand, carried by wind and water, literally gnaws the surfaces it touches. Thus the record-bearing strata that lie exposed are slowly ground to sand and dust, once more to be carried by water into the rivers and deposited in some new sedimentation at the river's mouth. Again, further diastrophic upheavals may cause great land masses to settle below sea level, where new deposits will form directly over ancient ones preserved from the grinding action of erosion.

The story is thus strangely discontinuous. Indeed the record of paleontology is something like a book written in words of stone — a book in many mutilated volumes. For after the first pages were laboriously written, in the course of some millions of years, many were torn and wrinkled, and many were destroyed. Often the story was continued in new pages superimposed upon the earlier ones that had been spared, and often early pages have been torn from their places and thrust in somewhere else. Only the most careful search has enabled the paleontologist to piece out

the record. The story is not yet fully known and perhaps never will be, but the results already achieved are something like a miracle.

How Fossils Are Formed

Fossils are preserved in a variety of ways. Occasionally entire animals have been preserved by unusual conditions, such as being trapped in an ice crevasse. Thus woolly mammoths, great beasts probably not extinct more than a few thousand years, have been found completely preserved, skin, flesh, bones and all, in regions of Siberia. Other creatures have become embedded in asphalt or in plant resins.

More frequently only the harder parts of animals have remained — skeletons, bones, chitinous or horny parts, and shells. Most abundant are the shells of mollusks and lampshells, which, like bones, are largely composed of mineral substances. The chitinous structures of creatures such as crabs and insects, are less common. Even though softer tissues of such animals usually disappear before they can form a permanent record, much can be learned from the skeletal remains.

Often the original structure is completely replaced by mineral substances which crystallize out of the water in which they are dissolved. This may take place with such microscopic accuracy as to yield a complete and perfect reproduction of the original, even to the point of revealing the shapes and sizes of individual cells and the very nuclei within them. At other times the organism may fall into mud or silt, where it eventually rots away, leaving only an empty mold. Later, under favorable conditions, this mold may be filled with a different material which eventually hardens to stone, thus producing a perfect cast of the original's outer form.

Even the tracks of animals that crawled or walked across a mud flat millions of years ago have been preserved. Footprints of dinosaurs have been found in abundance in some localities and are even sold as curios. From a footprint it can be told whether an animal walked on four legs or on two, whether it walked or hopped, whether it used its tail as a support while walking, and whether it walked on rela-

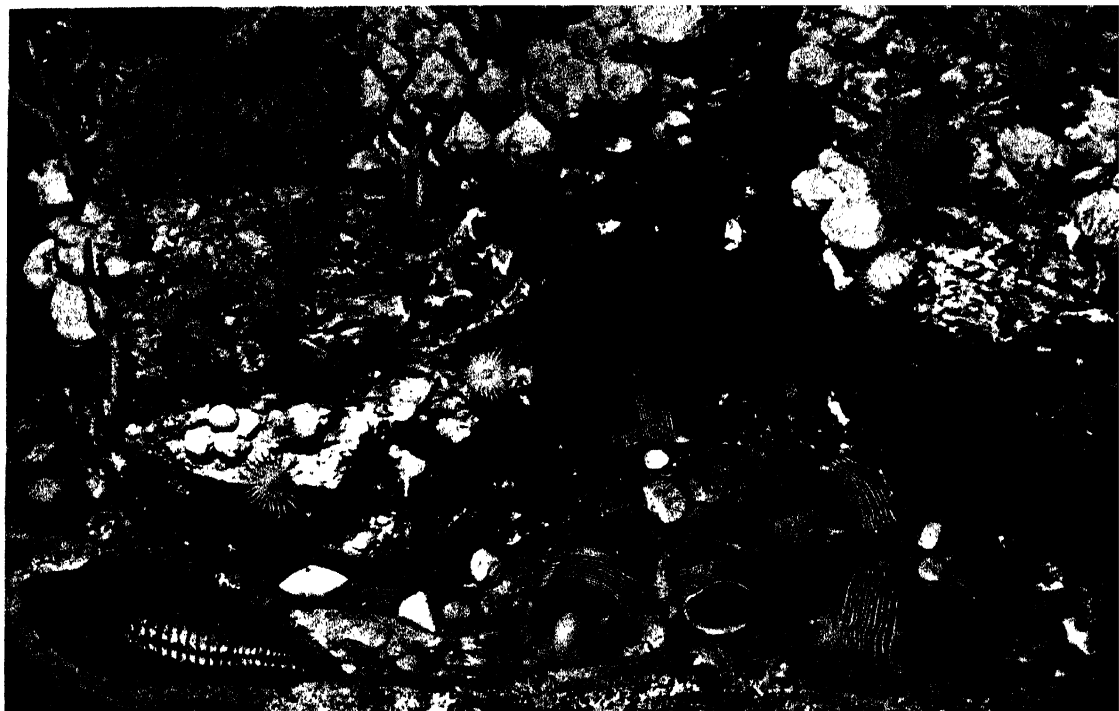


Fig. 69. Reconstruction of a Silurian sea bottom, with a group of trilobites.

tively dry land or frequented shallow lakes or ponds. Excrements of animals have been found, and may give evidence of feeding habits.

The immense variety of organisms that have gone before us becomes apparent when we consider that only the rare creature dies under conditions that make its preservation possible. Moreover, the thousands of fossils which have been found are but an infinitesimal fraction of those still hidden, and those extant are but a fraction of those originally formed.

What Fossils Show: General Considerations

Since the position of a fossil within a stratum may be a measure of its relative age, it is possible, by comparing organisms thus preserved, to form a picture of the progress of life through the ages. It is obvious that a bacterium is simpler than a fish, an earthworm than a grasshopper, a moss plant than a geranium or an oak. The great fact is that fossils become not only different, but generally simpler and more primitive as we penetrate the older sedimentary layers. Recent strata bear fossils of ani-

mals and plants that do not differ markedly from those which live today. In the older strata, birds and mammals become rare, and those which appear show only some of the outstanding features of these groups, until finally they disappear entirely. In still older strata, reptiles of the weirdest and most varied kinds represented the "upper crust" of living organisms. Finally all traces of backboned animals disappear.

In all these strata, however, in the youngest as in the oldest, smaller and simpler animals are represented. The evidence of the rocks does not indicate that all the simpler organisms of past ages evolved into more complex ones; it shows only that some of them did. This evidence raises a difficult problem. If it was not necessary for organisms to become more complex in order to survive, why did some do so and others not? This problem we shall investigate later. First, three examples will provide a basis for further inferences.

1. *The Trilobites and Limulus.* Approximately 500 million years ago there lived in the oceans great numbers of trilobites (Fig. 69),

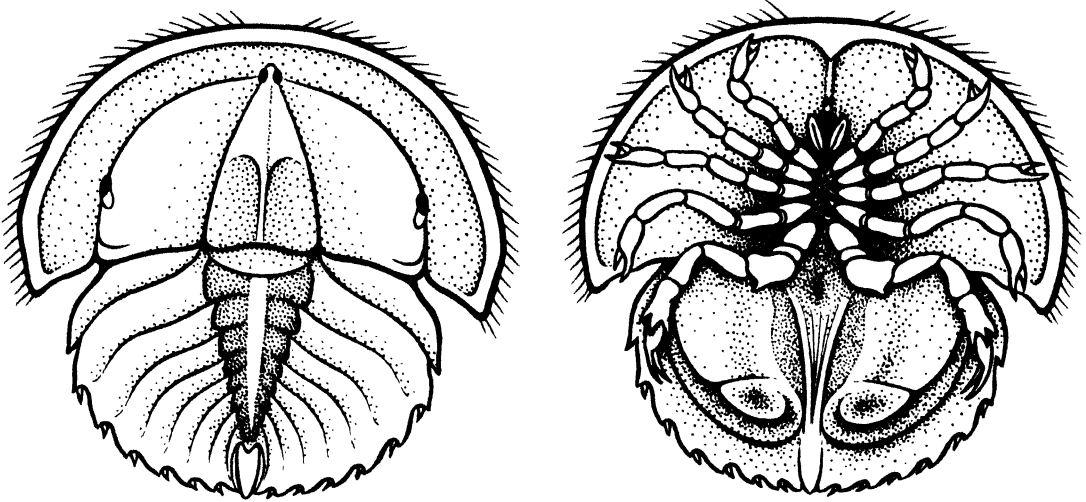


Fig. 70. *Limulus* larva, dorsal (top) and ventral (belly) views. General similarity to the trilobite is evident.

which looked much like giant sowbugs and ranged from a fraction of an inch to two feet in length. The trilobites represented the highest animal development of their age. No creature then alive surpassed them in complexity or in adaptation to environment. Their success is evidenced not only by their enormous numbers but by the great variety of forms in which they appeared. From one of these or from some related form, in the course of time, there sprang a new type, the arachnid, with characteristics which gave it novel advantages. The first representative of this group was the sea scorpion, or eurypterid. Another group arising from trilobite ancestry at about the same time was not nearly so formidable as the eurypterid, but was moderately successful. These, the Xiphosura, or horseshoe crabs, were rather like trilobites in general appearance. Gradually the supremacy of the trilobites waned; perhaps, as so often, from the competition of their progressive eurypterid descendants. The Xiphosura, too, gradually waned, but one representative of this order, *Limulus*, the present-day horseshoe crab or king crab, has survived, and has come down through the ages almost unchanged.

It is not clear why this primitive creature, often referred to as a living fossil, should have

been able to persist where all others of its clan have failed, but several facts in this history are of more than passing interest. One is the continued existence, in modified form, of a creature successful hundreds of millions of years ago. Another is that progressive individuals of a once dominant group may replace the remainder of the group. Most remarkable of all is that the *Limulus* of today lays eggs that hatch into larvae which resemble nothing so much as small trilobites (Fig. 70).

2. *A Missing Link: the Archaeopteryx.* In the lithographic limestone of Solenhofen, in Bavaria, there was found in 1861 the fossilized skeleton of an animal that was indisputably a bird, though to modern eyes a very peculiar one. The creature was named *Archaeopteryx* (Fig. 71), and its importance can hardly be over-emphasized. The deposits in which it was found are about 150 million years old — clear evidence of the antiquity of birds. The stone in which its bones are preserved shows the delicate tracery of its feathers. Though definitely a bird, it yet had teeth, clawed fingers on its wings, and tail feathers arranged like the leaflets on a fern frond, clearly indicating the presence of a long, bony, lizard-like tail-structure of a kind not found in modern birds. For even modern birds with strikingly long

"tails," like the peacock, have only a tiny stump of a bone in the tail, the entire magnificent train consisting of long feathers only. The feet of *Archaeopteryx* are characteristic bird feet, and this itself is worthy of remark. For the scaly skin of bird feet should remind us of the skin of reptiles, though it probably does not often do so because the very commonness of birds robs us of our ability to take notice. Indeed, the skeleton of *Archaeopteryx* without the feather imprints surrounding it would probably suggest that of a lizard: front appendages with clawed fingers, as well as hind ones; a long slender neck; teeth in a slender head; a long, thin, bony tail. All these are found in the lizard.

Even without the skeleton of *Archaeopteryx* the anatomical and reproductive peculiarities of modern birds would suggest their reptilian ancestry, and this would raise the question of

a missing link. For a reptile, say a lizard-like one, could hardly become a bird in one evolutionary step. A hypothetical and synthetic missing link between birds and reptiles would be a creature very much like this one. *Archaeopteryx*, then, is a "missing link" that has actually been found.

3. *The Horse's Foot: A Series.* A study of the newer strata shows that horses existed in the recent past, although they differed in some details from those of today. This indicates that the modern horse did not appear suddenly, but descended from ancestors now extinct. Deeper and older strata show a change in the animal, yet a change sufficiently gradual to leave us no doubt that it is still the same animal. The general similarity in structure is so great that each older form is quite clearly an antecedent of the next younger one. Yet back at the beginning of the series the tiny

Fig. 71. Fossil remains of *Archaeopteryx*. Imprints of feathers and bony tail are clearly visible.



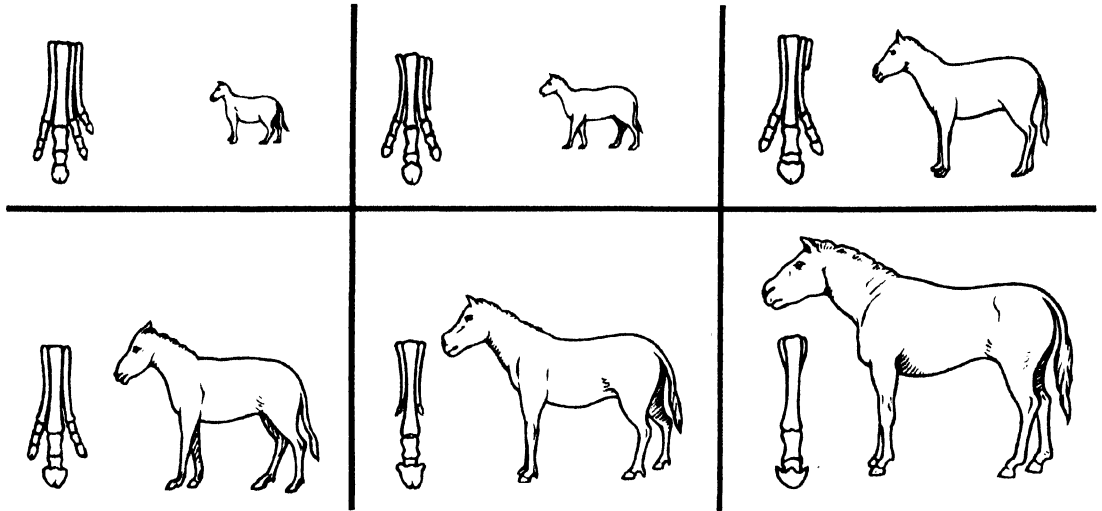


Fig. 72. The forefoot of the horse. The development from four-toed *Eohippus* (upper left) is clearly traceable.

Eohippus, the fox-terrier-sized "dawn-horse" of about 50 million years ago, so differs in size and structure as to be scarcely credible as the ancestor of the modern Percheron.

Although every feature of the skeleton tells the same story, the changes in the horse's foot are the clearest (Fig. 72). The horse's foot is almost perfectly adapted for running on hard ground but is practically useless for any other purpose. Most of his length of limb is due to the great over-development of the "hands" and "feet." The leg bones themselves are quite short and serve as powerful driving pistons for the long levers of the hand and foot segments. Where a typical mammal has five fingers, the horse has only the middle one, enormously enlarged and elongated. The end of this finger is expanded into a spade-shaped bone which supports the enlarged nail, or hoof. Attached to either side of this finger are two slender, functionless bony splints.

The origin of these splints becomes clear when we compare the limb of the modern horse with that of its earlier ancestors. *Merychippus*, of the late Miocene (about 12 million years ago), has two degenerated but unmistakable toes in the position of these splints. In *Miohippus* of the Oligocene (about 25 million years ago), the front toes are considerably larger relative to the middle toe, while in

Eohippus of the lower Eocene (about 45 to 50 million years ago), these toes are large enough to assist the third toe in supporting the weight of the animal. The forelimb of *Eohippus* had also a fourth and partially degenerated toe. We may conclude that a further tracing backward would lead to a five-toed ancestor, still undiscovered. Rudimentary toes in various degrees of degeneration can be observed in many modern animals, as in the foot of the modern pig and the hind foot of the dog. These may be considered as being on the same evolutionary level as the foot of the horse of twenty million years ago.

Conclusions

Paleontological evidence indicates that life on earth probably began about a billion and a half to two billion years ago. From the earliest periods no fossils remain, since early forms of life must have been exceedingly small and fragile, and the sediments from those periods have been subjected to much metamorphosis. Creatures such as viruses and bacteria could hardly leave recognizable fossil remains. But even in the oldest sedimentary rock which is devoid of recognizable fossils, there is some evidence of life in the form of calcareous deposits and oil, thin layers of carbon, and deposits of iron oxide, sulfur, and so on. In

younger strata there are increasing numbers of fossilized remains, beginning with worm trails and sponge spicules. Later appear whole casts and fossils, and with each successive stratum the collection of animals and plants assumes a more and more modern aspect. The next chapter will sketch in the outlines of this story, but first the other types of evidence for the theory of evolution should be considered.

THE EVIDENCE OF MUTATIONS

Evolution rests on change, but it is clear that the change is controlled, and that there is continuity from one generation to the next. Experience has taught us to expect kittens from cats and pups from dogs, and even to look for certain individual characteristics of the parents in the offspring. But experience has also taught us not to be surprised if the kittens prove to be different from the parents, or even different from all kittens we have ever known. As outlined in the previous chapter, hereditary continuity is achieved through the transmission of genes. These are, however, subject to the random changes, the mutations, which are prerequisite to evolution. The existence of mutations constitutes one of the most important evidences for the evolutionary theory.

That mutations actually occur has been demonstrated over and over again, not only in the casual experience of the farmer, but in the scientific laboratory as well. Thomas Hunt Morgan of Columbia University initiated the systematic study of gene mutations in 1910, and since that time millions of fruit flies (*Drosophila*) from carefully controlled stock have been individually examined for new mutations, of which some of the most obvious were in the shape and size of wings and in the color of eyes. These flies were a fortunate choice for numerous reasons. They are easily bred, they are prolific, they complete a life cycle in about three weeks, they have a highly differentiated exterior with many details that are subject to change, and a large number of them can be kept in a single half-pint cream bottle. In the course of this investigation, an average of

only about one mutation in every 50,000 flies was found, though it is probable that other mutations occurred which escaped detection. Thus it is clear that the mutant gene is exceptional rather than usual. Moreover, there is every indication that the mutations followed no plan, pattern, or discoverable line of development, but were completely random. For less than one-third of 1 per cent could be considered beneficial under normal conditions. In other words, out of three hundred or more, only one might represent an improvement. It is known that most mutations produce no visible effect at all, and their presence can be deduced only from lowered ability to survive, probably the result of chemical changes. Mutations or groups of mutations causing marked changes in appearance were very rare, and their potential usefulness even under altered conditions appears to be slight, since changes in appearance were usually associated with reduced viability, or ability to survive.

But the important fact is this: that all gene mutations are heritable, assuming of course that the individual in which they appear is able to survive long enough to breed. Thus the fact that there is mutation means that there is change; and change argues very strongly for the existence of evolution.

If we consider the number of mutations occurring in a species as a measure of potential change, then we may say that in general the mutation rate, though small, is sufficiently great so that the organism may change enough to fit changes in its environment but not enough to make it so genetically fluid that it could fit into no environment. The fruit fly, as well as innumerable other organisms, has shown that many mutations are rapidly eliminated, since they make the organism unable to survive in its environment. Still others are more slowly, though no less surely, eliminated by a somewhat milder lowering of viability. It is the exceptional mutation — an extraordinary rarity — that contributes toward the evolution of the organism; certainly not more than one in five or ten million. Hence it is little wonder that evolution is much too slow and gradual

to be "seen." Nevertheless, it has been amply demonstrated that the rare deviation from the standard stability of the gene — the mutation — supplies the genetic plasticity which makes possible the evolutionary molding of organisms. And in turn the proved existence of mutation is one of the strongest arguments for the theory of evolution.

EVIDENCE FROM TAXONOMY

The evidence provided by fossil remains and the existence of mutations provides some of the most cogent arguments for the theory of evolution, but there are other important kinds of evidence besides these. One of these is drawn from taxonomy, the branch of biology which deals with the classification of organisms. Some orderly arrangement of units frequently dealt with is of course necessary, but this can be of many kinds. It could be based upon the purpose of the classifier, or, more logically, on natural relationships. Living organisms could be classified according to size, color, or habit. Indeed, because these qualities are obvious, they were the first basis of classification used. Thus any animal that flew was a bird. But since butterflies and bats could come under that classification, as well as feathered birds, it was obviously not a satisfactory one. Likewise, anything that burrowed or crawled was a worm, and the word *vermin* (worm) is still often used to include such varied creatures as worms, insects, and even rats and mice. If an animal lived in the water it was a fish, and thus whales and porpoises (pork-fish) were classified as fishes, despite the fact that they are warm-blooded and air-breathers (Fig. 73).

Basis of Classification

The present system of classification was originated by Linnaeus, an eighteenth-century Swedish botanist and a man of great insight. Although he still believed that each organism owed its existence to a special act of creation, Linnaeus succeeded, on the whole, in classifying organisms according to true similarity in structure and form. We have already seen

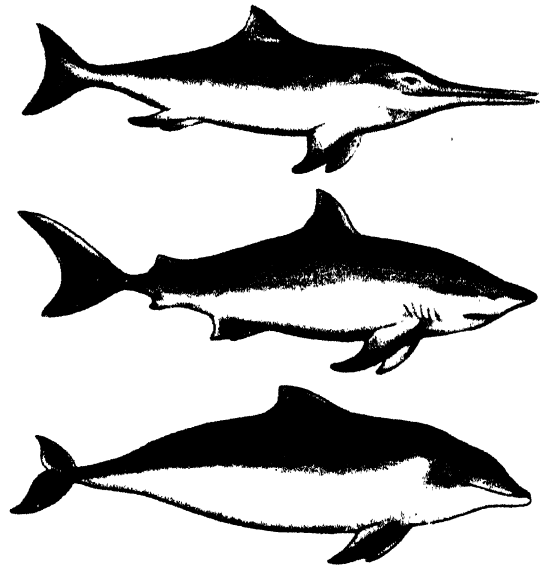


Fig. 73. Deceptive similarity of appearance between a reptile (*Ichthyosaurus*, top), a fish (shark, middle), and a mammal (porpoise, bottom): convergence in form due to environment.

that organisms descended from a relatively recent ancestor have many characteristics in common. Linnaeus saw that such groupings form natural kinships, even though he did not recognize the reason for their similarity. For instance, many animals have in common a high constant body temperature, are covered with hair, and bear live young which are nourished with a body secretion, milk. Linnaeus saw that, in classification, animals possessing these characteristics should be placed in one large group, the mammals. Similarly, the birds, being feathered, egg-laying, and warm-blooded, are obviously another natural group. The same holds true for the reptiles, scaled animals that lay leathery eggs which hatch lung-breathing young. Likewise, slippery-skinned animals which lay small eggs (generally under water) that hatch into gilled larval forms are recognizable as amphibians. Again, those that have fins instead of legs and breathe through gills form a distinct group, the fishes.¹

¹ A summary classification of both the plant and the animal kingdoms is given in Appendix A.

Implications of the System

At first such a classification was thought to imply special acts of creation. Indeed, there can be no argument that these groups were created — the argument is merely over *how* creation occurred. The modern scientist is not concerned with the concept of creation by a special act of an unknown force, and prefers to attempt a partial explanation in terms of known forces. For where sufficient evidence has been gathered, new forms appear not to arise suddenly, but always to be linked to the past through less specialized but similar forms that preceded them. Thus it is found that fish-like animals preceded amphibians, that these preceded reptiles, and so on. But we must not over-simplify and think of fishes generally as ancestral to amphibians, and these as ancestral to reptiles. For since modern amphibians and modern reptiles are contemporaneous, neither can be the ancestor of the other. In fact, modern amphibians have evolved along lines of their own and have frequently become quite as specialized and successfully adapted as many reptiles. The illusion of a consecutive evolutionary relationship stems from the fact that animals have not all evolved with equal rapidity in all respects. The evolutionary tree proves to be not a tree at all, but a profusely branched bush. Some organisms, the king crab and others, have persisted for hundreds of millions of years practically unchanged. Compared to many of their present contemporaries, these creatures are simple and primitive. Thus it is clear that complexity is not a necessary consequence of evolution, nor a requisite to survival.

But where marked change occurs and persists, it is generally accompanied by greater efficiency and frequently by greater complexity. It is this unequal rate of change which has resulted in the great variety of simple and complex organisms on earth today. Moreover, this diversity enables us to group organisms by ascending complexity — not in a single sequence, but in a multiple branching one. Thus we can trace lines from the simplest

bacteria or even the filterable viruses all the way up to the present end branches, the insects, mollusks, birds, and mammals. Such an arrangement of groups, classified according to common structure and arranged by increasing complexity (in but few cases is there a marked decrease in complexity), is the one accepted today.

Irregularities in Classification

Thus modern taxonomy is based on structural and genetic relationships implying descent and common relationship (phylogeny) which in turn are based on paleontology. The system is strengthened by the fact that while most organisms fit into established groups, there are certain non-conformists that fall halfway between. Thus certain worm-like creatures that also have insect characteristics fit exactly into neither group, but share the qualities of both. And certain mammals — the duck-billed platypus of Australia, for example — perform certain mammalian functions in a rather slipshod manner, and in other ways are suspiciously reptilian. Their temperature is more nearly constant and generally higher than that of reptiles, yet far from being constant. They produce milk, but do not have proper milk glands like other mammals. And they lay eggs, a habit abandoned by other mammals ages ago.

Even the animal and plant kingdoms are not proof against overlapping. Certain creatures are listed as plants in botany books and as animals in zoology books (*Volvox*, *Chlamydomonas*, etc.). Such anomalies are now considered as “plant-animals” and given under both categories, and biologists do not think of quarreling over the matter. It is merely another proof that since all organisms have descended from common ancestors, many of today’s man-made classifications will merge, even as all must when traced back into the past.

The Phylogenetic Chart

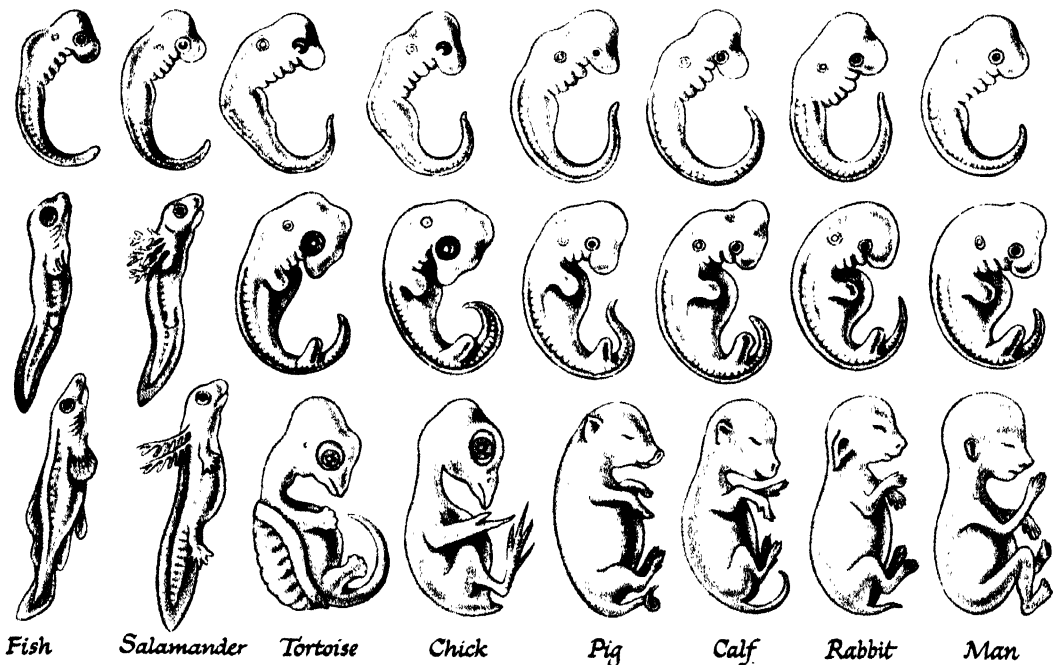
The most prominent groups of living organisms are shown in the phylogenetic chart (Gr., *phylon* = race, tribe) for animals and

plants, given inside the front and back covers of this book. In this chart, modern classification (taxonomy) is superimposed upon ancestral history (phylogeny). The chart should be studied and referred to often in reading later chapters of this book. For clarity the chart is greatly simplified; nor should too much emphasis be placed on the manner in which the various columns, representing modern groups, are joined at their bases, for we have far too little detailed and accurate information to be certain of exact relationships between major groups. This uncertainty is expressed in the haziness of the diagrams at such points. Somewhere within each pair of hazy lines would run a clear and sharp line if we knew all the facts.

The top line of the chart represents today. Each column that reaches the top level represents a type of organism that has survived to the present. The width of each column, or branch, represents in a very general way the numerical preponderance of an organism at a given point in time. A column that terminates before it reaches the top indicates extinction. Here and there the names of known an-

cestral forms of certain branches are indicated within the column representing that group. Horizontally, the modern groups are arranged according to degree of complexity. The *Schizophyta* (bacteria, etc.) form the central starting point. Marching up the animal branch of evolution (top border, left to right) are the *Protozoa* (single-celled animals); *Porifera* (sponges); *Coelenterata* (corals, sea-anemones, jellyfishes); *Mollusca* (oysters, clams, snails, squids); *Annelida* (segmented worms); *Crustacea* (crabs, shrimps, lobsters); *Merostomata* (the king crab, *Limulus*); *Arachnida* (spiders, scorpions); *Myriapoda* (centipedes); *Insecta* (insects); and *Vertebrata* (vertebrates). This does not represent the actual order of evolution, but an *approximate* order of increasing complexity. Outstanding exceptions are perhaps the mollusks, which have scaled heights of their own, and the myriapods, which really show less specialization than the arachnids. A glance at the base of each branch will reveal why they have been placed in the order here given. The main branch leading to the back-boned animals, the vertebrates, breaks off from the others far back in the Proterozoic. Thus

Fig. 74. Vertebrate embryos show marked similarity in early stages, increasing divergence later.



man's relation with the jellyfish is indeed remote. If the chart were more detailed, it would be studded with branches that end before they reached the top.

The plants can be traced up and across the chart in the same way as the animals, though they are here given in less detail.

EVIDENCE OF EMBRYOLOGY

Another body of evidence for the theory of evolution is supplied by embryology, that branch of biology which deals with the genesis and development of the embryo, the organism before birth. Karl Ernst von Baer, in working with vertebrate embryos, observed that they showed great similarity of structure in their early stages. On the basis of such evidence, the German biologist Ernst Heinrich Haeckel went a good deal further and formulated what he called the Biogenetic Law or the theory of recapitulation, which asserted that organisms recapitulate in their embryological development the earlier phases of their phylogenetic history (Fig. 74). Unfortunately, the principle as Haeckel stated it was far too sweeping, and hence has been discredited. The more valid view is that there is a degree of embryonic resemblance between related species, and hence there is more than a kernel of truth in the basic concept, though it cannot be pushed as far as some have tried to push it. When the term *recapitulation* occurs in this book, it is used to mean this kind of resemblance only.

Modern View of Recapitulation

The modern view is much as follows. Since evidence makes it clear that the more complex organisms of today evolved by gradual change from simpler ones, it is not surprising that we find structural remnants of early ancestors preserved somewhere in the life-history of the descendants. Such changes are based upon mutations in the genes, which may become effective at any phase during the development of an organism. A mutation may show its effect early, or not until a relatively late stage in the organism's development. Thus, in the

latter instance, the genes that control the resplendent adult plumage of the peacock do not perform their function until the third year after hatching. Hence if an animal experiences a mutation that will cause it to differ in the adult stage from the conventional pattern of its species, the individual may still be exactly like its non-mutant fellows throughout its early life. Now if an animal, changed by successive mutations, finally came to differ radically from its earlier form, some characteristics of the original form might finally become of little or no value to it. Such characteristics could be dispensed with, and if a mutation eliminated all or part of an obsolete structure, the descendants of such a mutant form would not show that phase of development. This might happen or it might not. Thus we should expect recapitulation in any organism to be a sketchy and not an unbroken review. Moreover, our interpretation of early developmental phases may occasionally be faulty. For these reasons the facts of recapitulation must be cautiously evaluated.

Embryonic Resemblances

In the earliest phases of their growth, all multicellular animals are remarkably alike. The single cell (the fertilized egg or zygote) multiplies by mitosis. First two cells are formed, then four, eight, and so on (Fig. 75). As the number of cells increases, they form a hollow ball, the wall of which is composed of a single layer of cells. By various methods, this ball becomes a structure of two cell layers surrounding a cavity, the beginning of the digestive tract. This structure then stretches and elongates, producing a worm-like tube with a double wall. At this stage appears the basic pattern of the animal-to-be. Further foldings, stretchings, and bulgings eventually produce the differentiation of the various organs and organ systems, until the organism is almost a complete miniature of the final product.

As these changes take place, the specific characteristics of the organism gradually appear, and increasing differences between various organisms become apparent. These events

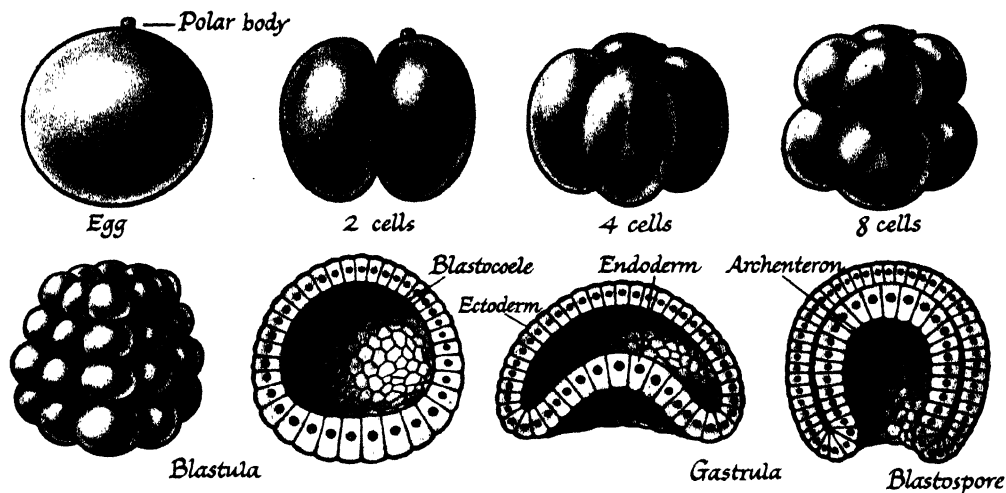


Fig. 75. Cleavage, first steps in the life of a multicellular organism.

have been studied in great detail, so that we know quite definitely what happens at each stage of the process. But we are often still ignorant of the causes of such precise and amazing evolutions. Even though there may be variations and modifications in the earlier stages, the differences are far less striking than the similarities.

If we now observe the course of the individual's development in relation to its history in the phylogenetic chart, the parallel is striking. Thus protozoa are single-celled creatures like the metazoan egg at the beginning of its career. Colonial organisms, mere clusters of undifferentiated cells, are comparable to the early multicellular phase of the embryo. The hollow ball, or *morula*, shows a striking similarity to the spherical *Volvox*, a colonial organism on the verge of becoming multicellular and differentiated. The double-walled ball, or *gastrula*, illustrates the basic body-plan of the coelenterates. Organisms just above this stage on the phylogenetic chart are worm-like in structure and may be compared to the worm-like phase of the embryo. In later phases of embryonic development, similar resemblances are numerous.

Evolutionary Peculiarities of the Human Embryo

Nor does the recapitulation of the general evolutionary pattern end here. In the human embryo, after the basic outline of vertebrate

form has been reached, in the fourth or fifth week of its development, several un-human peculiarities appear. In addition to certain negative qualities, such as the absence of a face and the lack of human shape and form, as exhibited by the mere budding stumps that foreshadow arms and legs, there are positive qualities generally associated only with lower organisms. The embryo at this stage has an indisputable tail, large and well developed. The fact that the tail begins to regress in the seventh week without ever serving any apparently useful function makes it all the more noteworthy. Figure 74 shows that the tail is a normal adjunct of all other vertebrate embryos, as we should expect, since it is retained in the adult. The presence of a tail in the human embryo supports the inference already drawn from the evidence of paleontology: that ancestral forms of human beings had tails.

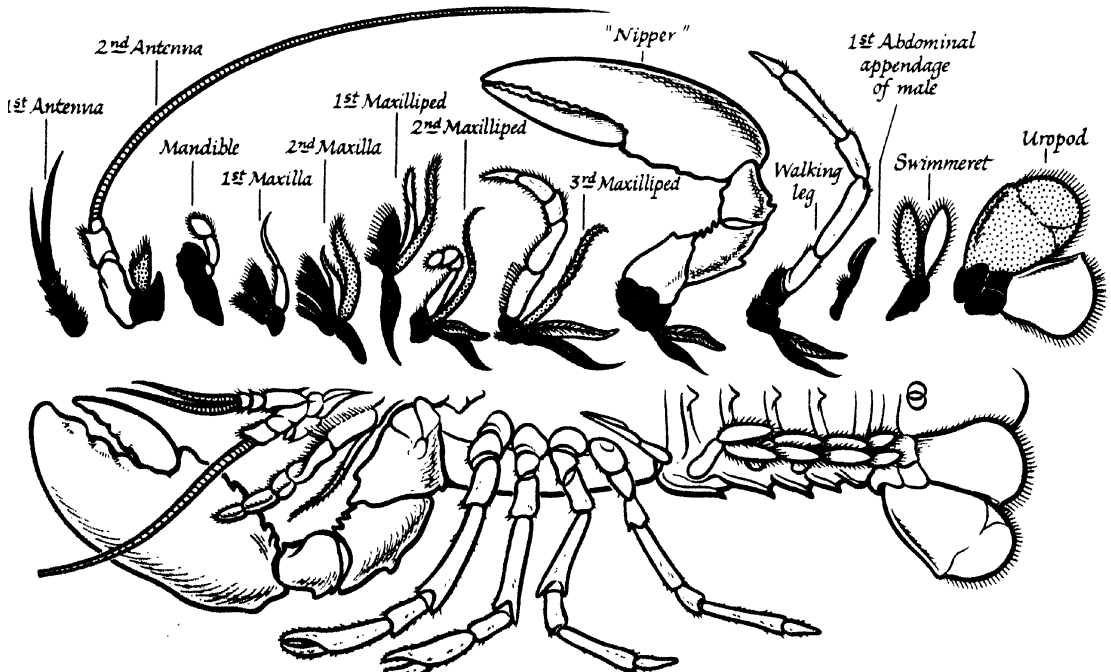
In the human embryo there are also folds and creases in the neck region, called branchial grooves and arches. The history of these leads back even further. Later these folds become changed and incorporated into the most varied structures — parts of the jaw, tongue, throat, and ear. But the embryonic fish, in a comparable stage of development, has the same folds and creases, although the fish never produces many of the features to which the branchial arches give rise in the human em-

bryo. Indeed, in the fish embryo most of these arches become separated by the transformation of the grooves into gill slits, and become directly transformed into the gills, the breathing organs of the mature fish. Careful examination of the branchial arches shows that this was their original function, and that the varied structures into which they change in the human embryo are later developments. Figure 74 shows that the other vertebrate embryos bear the same gill pouches, although only the first two forms shown ever use them in breathing. The various stages in the embryos of higher organisms resemble not the adult forms of lower ones but the present embryonic forms. In subsequent stages both develop in separate directions.

As we learn more of the details of organ formation, it becomes increasingly apparent, wonderful as it is, that nature's way of building is much like that of the Yankee farmer putting together home-made farm implements. Both use whatever parts and materials are available, regardless of their original function. In the human embryo there are several structures which serve no function. One of these

is the yolk sac. Yolk sacs are produced in the embryos of many animals and hold the yolk, a substance incorporated in the egg at its formation to become food for the growing embryo. The human embryo, nourished by osmosis from the vascular tissues of the mother, receives very little yolk. Yet it grows a yolk sac, which remains empty and has no function. The human embryo grows a coat of silky hair, the *lanugo*, which appears in about the fifth month, is prominent in the seventh, and usually disappears in the eighth. This too has no function, but it sometimes persists after birth, especially in the fine down on the faces and necks of women, though normally coarser hair replaces it. Then also, the human embryo early develops kidney tubules (the *pronephros*) which never function and are swiftly replaced by a more advanced kidney structure, though in lower vertebrates this becomes the active kidney. Often in higher organisms, however, these functionless embryonic structures are necessary predecessors to those which develop later. Were it not for the primitive kidney, for instance, the more complex functional one could perhaps never develop in the human

Fig. 76. Homology in the appendages of a lobster. Each specialized appendage was derived from the same primitive appendage pattern. Shading designates origin of parts: black, from upper joint (protopodite); stippled, outer fork (exopodite); white, inner fork (endopodite).



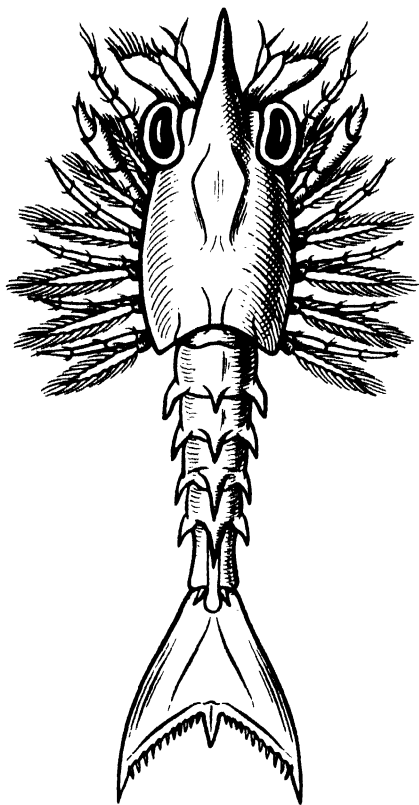


Fig. 77. Larval stage of lobster, showing primitive forked appendages.

embryo. These are but a few instances of many which strengthen the assumption that ontogeny, the development of the individual, presents a brief and partial recapitulation of its phylogeny.

Crustacean Affinities in Larval Forms

Despite the great diversity in form and size between the various forms of adult crustaceans, there are clear indications of relationship in the early developmental forms, especially in the larvae.¹ Adult crustaceans may vary in form from lobster to barnacle, or to the sac-like shapelessness of the parasitic crustacean, *Sacculina carcini*. They may vary in size from almost microscopic copepods, such as *Cyclops*, to giant Japanese crabs, with a leg spread of

about ten feet. Yet many crustaceans have preserved in their remarkably similar larval forms the evidences of their common and primitive ancestry. A study of their appendages affords an excellent opportunity to observe this evolutionary relationship.

Anyone who has dissected a lobster on the dinner-plate will know what a formidable array of appendages he has to deal with (Figure 76). Careful study of their embryological development (best not attempted on the dinner-plate) shows that their appendages are all derived from a basic and simple two-forked appendage found generally among crustaceans, but most common in the lowest forms. That all the varied appendages of a lobster — its antennae, claws, jaws, feet, swimmerets, and tail-parts — should have derived from this common basic structure is a striking fact, yet this same sort of specialization occurs in a host of other organisms, and is referred to as the principle of *serial homology*, because the organs are arranged in a series upon the body. The front and hind limbs of a mammal afford an additional example of serial homology.

Most crustaceans pass through one or more larval stages, the earliest and most primitive of which is called the nauplius. Some of the higher crustaceans, such as the lobster, hatch at a stage more advanced than the nauplius, a fact quite in accord with partial recapitulation. But even in the lobster, the advanced larval stage still has appendages of the characteristic forked structure (Fig. 77). The striking similarity of the nauplius larvae of widely differing crustaceans can be explained only in terms of common ancestry (Fig. 78). Of the various crustaceans shown, several differ so widely from the standard pattern in their adult forms that zoologists would find it most difficult to classify them at all, but for the evidence of their larval structures. Thus the barnacle, *Lepas*, was formerly classified as a mollusk because of its superficial similarity to some of these. A closer study of its anatomy reveals its crustacean affinities, and its larva supports this evidence. No amount of careful anatomical study would aid the zoologist in

¹ For a definition of this term, and of many other terms used in this book, see Appendix B.

classifying *Sacculina* (Fig. 79), but even a layman, glancing at its larva, would be able to see that it is similar to that of other crustaceans. Thus the nauplius larva of the crustaceans is an important piece of evidence in support of the phylogenetic relationship of organisms; in short, of their descent with change from a common ancestry.

Further relationships among crustaceans,

Fig. 78. Nauplius larvae (below) and corresponding adult forms (right). Top to bottom: *Lernaeocera*, parasite on fishes; *Peneus*, free-living; *Lepas*, goose barnacle; *Cyclops*, common in fresh water.

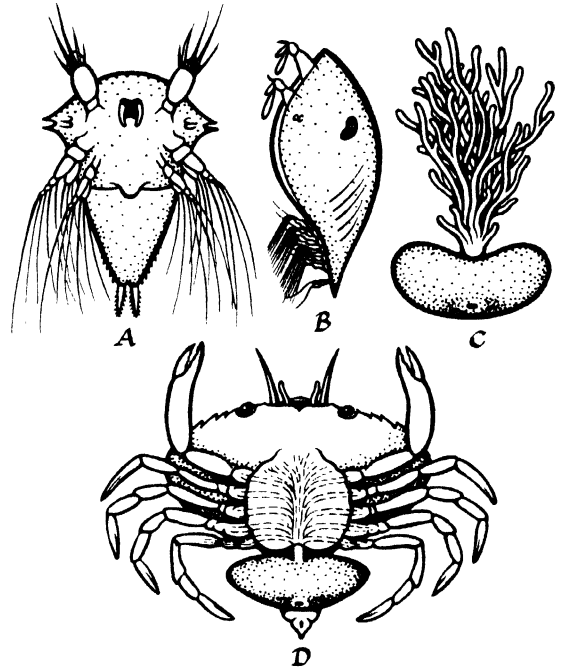
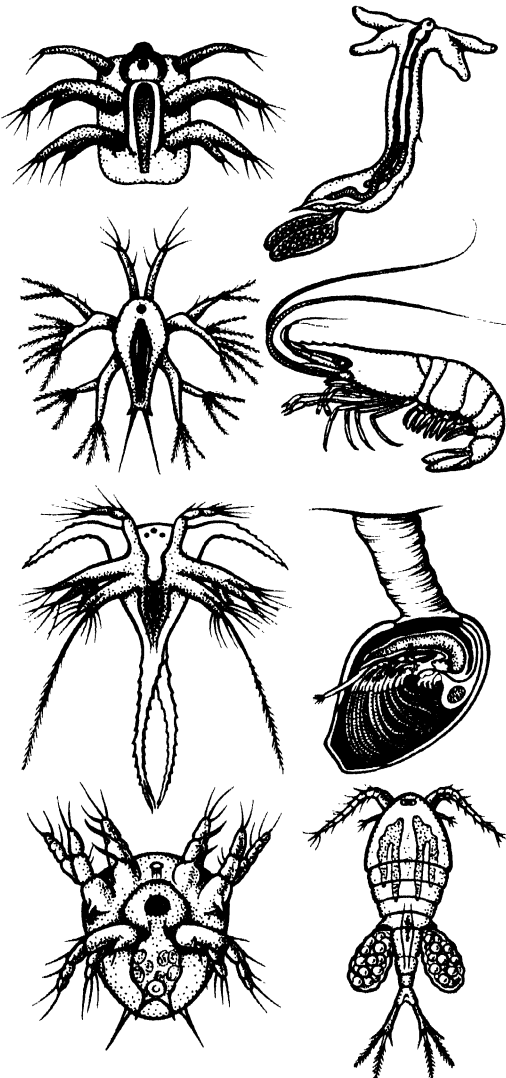


Fig. 79. Life history of *Sacculina carcini*, a parasitic crustacean. A. Typical nauplius larva. B. Cypris stage, lateral view. C. The adult *Sacculina*, removed from host, shows no vestige of crustacean affinity. D. The sac-like body of *Sacculina* protruding from the abdomen of its host, the blue crab.

and between these and other arthropods, may be established. Thus simple crustaceans, such as *Branchipus*, show structural affinities to the extinct and fossil trilobites (Fig. 68). Trilobites, in turn, have many points in common with the king crab, especially with its larval form. The king crab, in its turn, is definitely allied to scorpions and spiders. Thus another chain of phylogenetic relationship may be established through larval forms.

Many other marine organisms that vary widely in adult form, like the crustaceans, have remarkably similar larval stages. And again there is reason to suspect that this larval similarity indicates common ancestry. But mere similarity in form must not be construed as positive proof of relationship. The shark (a fish), ichthyosaur (a reptile), and the porpoise (a mammal) show a remarkable similarity in form (Fig. 73, page 106). Theirs is the only form which is efficient for the type of life they live. A closer examination of these three ani-

mals shows clearly that they are not at all closely related but belong to three different classes of vertebrates. Such superficial similarity in form, which is a result of a selective environment, is known as *convergence*. Before we conclude, then, that similarity of larval forms is proof of relationship, we must have other evidence. Further examination of other marine larvae furnishes this proof.¹

Larval forms resembling more primitive ancestors, or at least the immature stages of such ancestors, could be listed almost endlessly. Cases familiar to almost everyone are the tadpole with its fish-like characteristics, the caterpillar which resembles the worm-like ancestors of the insects, and the maggot of a fly, similarly reflecting a worm-like ancestry. That organisms reveal phylogenetic relationships during their embryological development appears to be established beyond a doubt.

EVIDENCE FROM COMPARATIVE ANATOMY

Homology in the Leg of the Frog

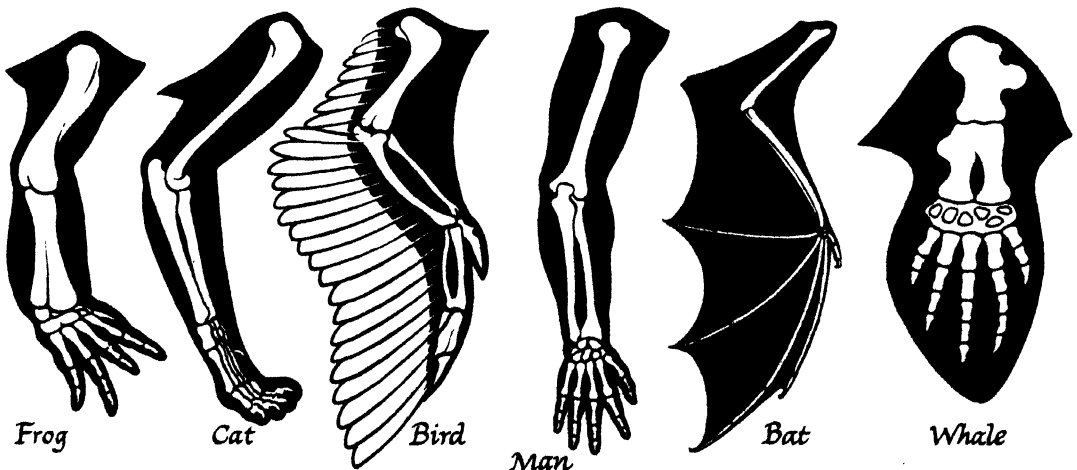
The classification of animals and plants is based upon similarity of fundamental struc-

¹ See page 312 for a discussion of the type of larva called a *trochophore*, on the basis of which it has been possible to establish a relationship between such different groups as wheel animalcules, earthworms, and oysters.

ture, and thus, in each group, the members possess similar or *homologous* organs, having the same origin and the same basic structure, though often modified for totally dissimilar uses in the different species. But however great this modification, the underlying homology remains apparent. These similarities constitute still another body of evidence for the theory of evolution.

Thus the leg of a frog is an ingenious mechanism apparently designed and executed for the performance of its special functions (Fig. 80). Yet essentially the same structure is found in the leg of a cat, the wing of a bird, and the arm and hand of man. Within the leg of the frog, which is a mass of effectively arranged muscle tissue, is a rigid framework of bone. If there is anything astonishing about this framework, it is only that it appears so well suited to its purpose. At the top of the foreleg is a single long bone, the humerus, with a ball-like upper end that fits neatly into a flat, curved bone, the scapula. At its outward end, the humerus forms a joint with another long bone, which appears to be a fusion of two, side by side, the radio-ulna. The humerus and radio-ulna are articulated at the elbow. At the outer end of the radio-ulna are a number of small wrist bones to which are attached five chains of bones forming hand and fingers. The elbow and wrist permit flexibility, while the long bones provide the rigidity which enables the

Fig. 80. Forelimbs of some vertebrates serve widely differing purposes but show the same structural pattern.



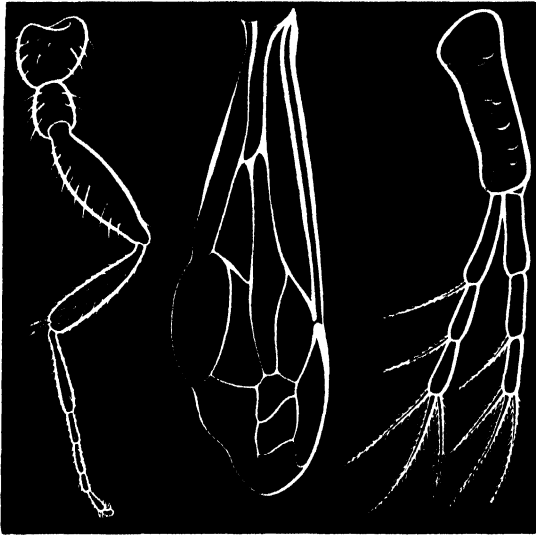


Fig. 81. Invertebrate appendages. Similarity in function does not demand similarity in structure.

leg to carry a load. Fingers, five in number, though one is strangely crippled, give traction and enable the frog to manipulate its body. All in all, the leg is well constructed, and were it the only one available for study, we might well conclude that nature evidently requires just this sequence of bones to achieve that particular job. Yet the basic structure of the fore limbs of many other creatures shows the same basic structure, however modified. And the more highly specialized hind leg of the frog — and of the others — has an exactly similar sequence of bones, once again illustrating serial homology.

Other Cases of Homology

The foreleg of the cat is remarkably like that of the frog, but has a few added refinements. Radius and ulna are separate, giving a flexibility which the leg of the frog does not possess. The cat also stands on its toes, so that its wrist is elevated from the ground. But there is no fundamental difference.

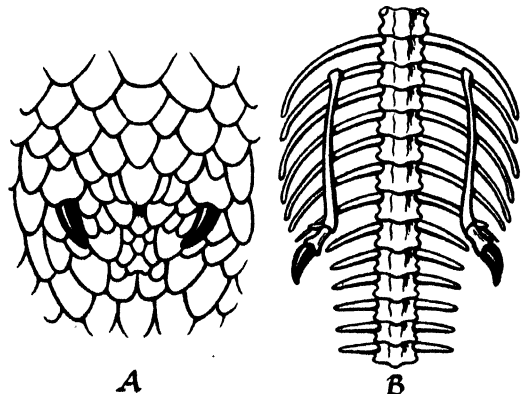
Even if the similarity in the legs of the cat and the frog could be accounted for by similarity in function, we should not expect similarity in the limbs of many other animals, since they

serve the most varied uses. The system of bone formation which is ideal for support and manipulation could hardly be ideal for flying or swimming. In the walking, flying, and swimming appendages of invertebrates (Fig. 81), a totally different architecture provides high efficiency. Nor has size anything to do with the matter. Many invertebrates are considerably larger than some vertebrates. The hummingbird has the same arm construction as the whale, but one wholly different from the wing of giant insects which equal or exceed it in size. Thus it is evident that the homology of the appendages, and of all the other bodily structures of different vertebrates, must be due to some other cause than their adaptation to function. Only the concept of genetic relationship, through the principle of evolution, offers a satisfactory explanation.

Rudimentary Organs

Even more striking indications of ancestral relationship are rudimentary organs, found in many classes of organisms. Snakes, for instance, have no appendages, though “hips” with attached remnants of hind legs appear in the python (Fig. 82). The fact that these structures have a use as copulatory organs or claspers may account for the fact that they have not completely disappeared in these snakes. Similarly, the remnant of the ulna in the arm of the bat (Fig. 80), of the metatarsals in the foot of the horse (Fig. 72), and of the fifth toe in the front foot of the frog, all indicate

Fig. 82. Vestigial hind limbs in python. They have survived because they still serve a function. *A.* Ventral view, exterior. *B.* Skeletal view of the same.



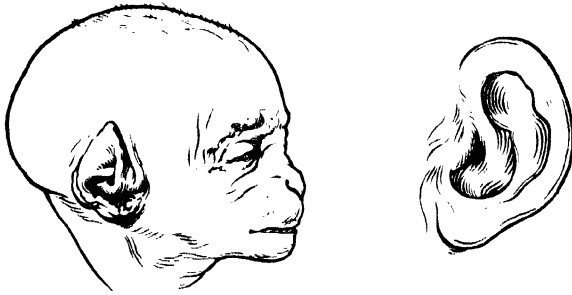


Fig. 83. Ear of fetal orangutan and human ear.

a common ancestry. A peculiarity of the human ear, the little point of gristle just above the lobe offers an interesting comparison with the structure of the ear of the foetal orangutan (Fig. 83). It appears to be a remnant of a pointed ancestral ear.

Integument and Other Structures

Comparison of the integument, or covering, of some classes of vertebrates also reveals a common origin. The skin of vertebrates consists of two layers of differentiated cells, the outer layer or epidermis, and the inner, or dermis. Scales in fishes and reptiles are produced either from the dermis alone or by the two skin layers in combination. The two layers produce the peculiar scales of the shark in a manner quite similar to the way vertebrate teeth are formed. Does this imply that teeth are modified scales, or vice versa? Actually, observation shows that the teeth of sharks are but scales drawn into the mouth, and this makes it reasonable to regard the teeth of the higher vertebrates as having a similar origin. Feathers of birds, also, are highly evolved and differentiated scales similar in origin to the scales of fishes.

Cases of similarity in structure not based on similarity of function are innumerable. The neck of the giraffe, of the elephant, and of the mouse, each has just seven vertebrae. The leg of the stork has the same bone elements as the leg of the hummingbird. The immobile human ear has sets of muscles around and within it basically like those around the mobile

ear of the horse. The biting parts in the mouth of the grasshopper, the sucking ones of the mosquito, and the lapping ones of the housefly, are made up of the same elements, shaped according to the work required of them in each case. The whale has a pelvic girdle and rudiments of hind legs, thus by a slight token maintaining its status as a quadruped.

Further evidence that the fundamental similarities are those of structure and not of form is found by making a comparison of the foot of the mole, a vertebrate, with that of the mole-cricket, an insect (Fig. 84). Each has evolved an efficient digging organ, with a resulting convergence of form, but the two are quite different structurally. The same principle accounts for the amazing similarity between the eye of the vertebrate and that of certain mollusks, such as the octopus. So similar are these two organs that the eminent English biologist Mivart considered them as evidence against the doctrine of evolution, but his views are not generally shared today.

EVIDENCE FROM COMPARATIVE PHYSIOLOGY

A full understanding of the nature of the tests with which we shall deal under this heading would be possible only after extensive studies in chemistry and physiology. It is quite possible, however, to grasp the general principles involved without such preparation.

From one point of view, the living organism may be considered as an enormously complex chemical machine. It follows that the peculiarities of one organism or another lie within the chemical differences between their cells, and hence that there are many different kinds of protoplasm. The difference between the cell of a maple tree and the cell of a cat is not one of appearance only; the protoplasm of the two differs in chemical composition, primarily in its proteins.

Grafting

These differences become quite apparent in horticulture. A method widely used in the

propagation of trees and shrubs is grafting, which consists simply in causing a twig or bud of one plant to grow upon the roots or branches of another. A tree produced by grafting a twig of one kind on the root of another will have the same characteristics as the one from which the twig was cut. Because of the re-shuffling of genes in sexual reproduction, a tree grown from a seed may not be depended on to produce another tree of like quality. By grafting, however, the quality is assured, except where there are inter-effects between graft and scion. But it is not possible to graft any twig on any variety of root. Twig and root must be related, or their union will not take place. Cells showing marked differences in structure and form will be chemically different. The ease with which a twig will grow upon a strange root is determined largely by the closeness of relationship, and of chemistry, between the two plants. Thus similarity in appearance, upon which relationship is judged, is verified by similarity in chemical structure.

Immunology

One of the clearest examples of chemical similarity is presented by sensitized sera.¹ Our bodies may produce protein substances which protect them against the greatest variety of

¹ A serum is the clear liquid obtained by permitting blood to clot and then removing the clot.

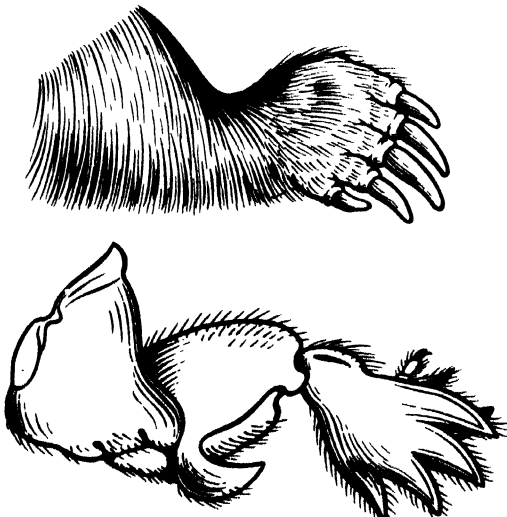
potentially harmful chemicals. The branch of medicine called immunology is based upon this fact. Exposure to chemical substances generated by disease-producing organisms (toxins) may cause the tissues of our body to produce protein antibodies, which tend to neutralize the harmful effects. Antibodies are produced not only to counteract bacterial toxins, but many other chemical substances. But the body sometimes produces much too violent a reaction for its own good. Asthma, hay fever, and a host of other allergies are the result of such over-compensation. In such a condition, the body is said to be sensitized.

After repeated small injections of human blood, the blood of a suitable test animal, such as a rabbit, will eventually be found to contain antihuman blood-proteins. Thus the rabbit has become sensitized to human blood. Blood serum taken from a sensitized rabbit will form a cloudy precipitate if human blood serum is added to it. Significantly, the same reaction, though weaker, results if blood serum from one of the great apes is added instead of human serum, while serum from most other types of animals yields a negative result. Thus we must conclude that the blood of the great apes has a chemical similarity to human blood greater than that of other groups, and that the similarity between the great apes and man is not limited to physical and anatomical resemblance alone. A similar kinship may be shown between the chemical composition of the dog and the wolf, of *Limulus* and the scorpions, and among many other groups. In fact, this type of analysis has proved to be of great help in clearing up cases of doubtful relationship.

EVIDENCE FROM DOMESTICATED ANIMALS

Domestication has produced such profound changes in animals and plants that one cannot but wonder why the concept of evolution was so slow in replacing a general belief in the fixity of species. The heritable changes taking place before our very eyes are strikingly displayed

Fig. 84. Digging feet of mole and cricket



by many species of domesticated animals. Comparison of a Newfoundland dog with a Pekinese, or of a Great Dane with a toy fox terrier, or of any of these with the relatively "unspoiled" German shepherd or police dog, shows the concept of the immutability of organisms to be a strange one indeed. Blood tests, susceptibility to the same diseases and parasites, and mutual fertility, all show the close relationship of these breeds, in spite of their dissimilar appearance.

Breeds and Species

There can be no question that organisms change, but there has been much controversy over the significance of the observed changes. It has been argued that by domestication man can produce striking superficial differences, but that these fall short of those which distinguish species. Critically examined, the argument appears to have little real significance, for it is now apparent that the grounds upon which a systematist distinguishes one species from another are quite arbitrary. Indeed, Dr. Tate Regan, at a meeting of the British Association, gave the following illuminating definition: "A species is a group of animals that has been defined as a species by a competent systematist." Generally the inability of two groups of animals or plants to interbreed successfully is considered sufficient reason to classify them as separate species. But this is purely arbitrary from the standpoint of taxonomy, as is shown by the fact that some mutually sterile groups show but slight visible difference in structure, while others showing marked structural differences may be mutually fertile. Furthermore, although all dogs, for instance, are classed as belonging to a single species, the cross-mating of some breeds produces deformed and virtually inviable offspring which could certainly not survive in nature. If interfertility were the criterion of species, separate species might well be established from some groups or breeds of domesticated dogs. On the other hand, numerous examples of animals classed as separate species are capable of mutual interbreed-

ing. May we not then say that evolution has occurred in man's own backyard and under his own guidance, even to the point of producing breeds with differences so great that if they occurred in nature they might be classed as separate species?

That some natural species show little difference other than mutual sterility merely emphasizes the arbitrary nature of classification. But viewed from the standpoint of evolution, such sterility is of major importance, for it isolates the two groups from each other, thus almost assuring further divergence. If man, by arbitrary selection, has been able to create different domestic creatures, what is to prevent nature, by other forms of selection, from achieving similar results?

Some Man-Made Variants

And certainly man has created some startling divergences, in chickens, pigeons, canaries, goldfishes, horses, and many other animals. Chickens come in almost every color but green. They vary in size from the tiny Bantam, no larger than a pigeon, to the Brahmin, about as large as a goose. They may have practically no tails or they may have tails yards in length. Some have been bred for blind courage and enormously long, strong legs; others have been transformed into egg-laying machines with an unbelievable digestive capacity. From primitive types that laid perhaps a few dozen eggs a year, hens have been produced that will lay well over three hundred eggs a year. Modern turkey breeders, within the brief period of the domestication of the American wild turkey, have created a bird that differs considerably from its prototype. Catering to the public demand, squat, wide-framed, dwarfed turkeys with all white meat have been created, since the older type of turkey was too large to fit into the average kitchen oven.

Pigeons, canaries, and goldfish have been bred for the most bizarre tastes. There are humpbacked canaries, white canaries, canaries with a chronic strut, some with caps and frills, yellow canaries, and common green ones. Pigeons with the most unusual specializations



Fig. 85. Fancy breeds of pigeons: fantail, pouter, and tumbler.

have been produced. Many of these new creations are obviously unfit for any other life than the domestic, for only under the protecting hand of man can they preserve the impractical structures and mannerisms that distinguish them. Tumbler pigeons turn somersaults as they fly. Some have been bred to such a degree of "tumbling" that they will senselessly abandon themselves to a series of somersaults even when not flying. The fantail pigeon not only constantly spreads its tail like a strutting peacock (Fig. 85), but in addition appears, especially when excited, to be completely at the mercy of convulsive "pouting" urges, which cause it to thrust out its chest, withdraw its head, and lean back so far that at times it loses its balance and tips over backwards. The impracticability of such a reaction pattern shows itself at feeding time.

Horses have been bred that weigh over 2000 pounds, and others that weigh only a few hundred. Fruit flies have been produced without wings, while others have four wings instead of the usual two—a significant fact, since the very class to which the fly belongs is the Diptera (two-winged), as distinguished from other classes of insects with four wings.

Domesticated animals represent an arbitrary development from abnormal individuals selected for breeding because their abnormalities were useful or desirable to man and

proved to be heritable. It must be emphasized, however, that the useful abnormality is a rare occurrence among a vast number of undesirable ones. Thus featherless pigeons, which do not have to be plucked, might be useful, but they are difficult and expensive to raise, since the loss of the insulating outer covering makes them extremely delicate. Indeed, like hairless calves and mice, they would hardly survive long enough to be found, except under conditions of domestication.

Some mice show a grotesque overgrowth of the skin coupled with hairlessness, a type that has been called the "rhino mouse." Pirouetting mice that whirl incessantly have been bred, and a herd of goats exists in which all the animals fall to the ground with rigid legs when suddenly frightened.

Effects of "Domestication" in Man

Nor are such abnormalities restricted to domestic animals. Man too lives under domesticated conditions and is subject to the same forces. Two samples of human hereditary variation may suffice to illustrate the point. One is the malformation of hands and feet (Fig. 86). The other is albinism, the hereditary inability to produce pigmentation, a defect which occurs occasionally in practically all types of organisms. Under ordinary conditions its victims are relatively short-lived,



Fig. 86. Hereditary malformations of hands and feet: "lobster claw" and "cloven foot."

either because they are conspicuous or because they may be weaker than their fellows (Fig. 87). Since changes of this kind are hereditary, they might become fixed in a new race if the individuals possessing them became isolated. In time such changes would be joined by others, and presumably the individuals which possessed them would ultimately pass the threshold that separates one species from another. There appears to be no fundamental difference between the nature of the initial, arbitrarily directed changes found in domestic animals and of the mutations that form the basis of the natural process called evolution. Indeed, both are forms of evolution.

Conclusions

The concept of evolution is the master key to many of the secrets of life. There

is hardly a new fact or idea that does not gain added significance in the light of this concept. Yet evolution is a groping, empirical process, executed with a lavish disregard for cost in life and material. The whole world is its laboratory, and all of earth's history has been at its disposal. Uncounted thousands of blind experiments have failed for each one that achieved even a temporary success. By far the greatest number of ventures proved to be failures and were snuffed out. No observer could have predicted, at any one moment in the history of life, which branch would win through to ultimate success. The most superficially promising branches frequently came to a swift and ignominious end. In view of what is now known of the evolutionary process, biologists are to some extent able to predict the kind of creatures which are likely to survive under certain conditions. On the basis of the evidence, it may in general be said that those organisms will tend to survive which are not highly specialized for a circumscribed environment. Certainly one could have been fairly certain that the once mighty dinosaurs, because of their extremely high specialization, would not have survived an extensive change in environment. On the other hand man, who is highly adaptable and strikingly unspecialized, is a likely contender.

Fig. 87. Albinism in a family of Negroes. Mother, albino; father, pigmented; child, albino. A study of this family suggests that in some cases albinism may be a dominant characteristic.



The Story in the Rocks: A Survey

Perhaps there is no better means of picturing the broad outlines of the history of life on earth than by surveying the major events that have taken place in the billion and a half or two billion years since life on this planet began.

Paleontologists have divided various levels of the earth's sedimentary deposits into geological eras reckoned in millions of years. To visualize these enormous spans of time, we may return to the analogy of the book of many volumes. If each word, line, page, and volume represents a metered amount of time, and if the approximately two billion years of the history of life fill twenty volumes, we may begin to see things in proportion. If we allot 100 years to the word, then:

a line of 20 words = 2000 years,
 a page of 50 lines = 100,000 years,
 a volume of 1000 pages = 100 million years,
 a set of 20 volumes = 2000 million years.

The whole span of recorded human history — about 6000 years — would be covered in the last three lines of the last page, and the history of the entire Christian era in the last line. Columbus would have discovered America just four and a half words from the end, and the Declaration of Independence would have been contained in the next to the last word.

The time-span since the probable beginning of life has been divided into five great *eras*. These are subdivided into *periods*, which in turn are subdivided into *epochs*.

The geologic eras and periods since life on earth began may be listed as follows:

Archeozoic Era

Proterozoic Era

Paleozoic Era

Cambrian Period
 Ordovician Period
 Silurian Period
 Devonian Period
 Carboniferous Period
 Permian Period

Mesozoic Era

Triassic Period
 Jurassic Period
 Cretaceous Period

Cenozoic Era

Paleocene Period
 Eocene Period
 Oligocene Period
 Miocene Period
 Pliocene Period
 Pleistocene Period
 Recent Period

The following pages illustrate some of the dominant forms of life in each era or epoch in so far as they can be reconstructed from the evidence of paleontology. Absence of an organism from any given scene does not indicate that it did not exist at that time, but only that it was not new or dominant then. Thus in general the lowest forms of life now in existence were among the first to become established, but in succeeding ages these were outdistanced by others which continued to develop.



ARCHEOZOIC ERA (Vol. 1 to Vol. 8)

This was a great period of mountain building. The earth was young, and at the beginning, rain falling on hot rocks probably formed masses of steam and vapor. Hot springs were no doubt numerous, many with high mineral content. Volcanic action and violent rains probably caused severe electrical storms.

Except for some possibly slimy and discolored films, the unaided eye could have detected no trace of life. Microscopic examination might have revealed some of the simplest of organisms, preceded, probably, by abiotically formed organic compounds or autotrophic bacteria; later, perhaps some green flagellates — single-celled creatures capable of carrying on photosynthesis. Deposits of car-

bon, in the form of graphite, suggest the presence of simple algae. Since animals must live on other forms of life, animals could not have appeared before other organisms, although limited organic resources were available. It is impossible to say when the first act of violence by one living organism was directed against another, but when one cell appropriated the protoplasm of another for its own purposes, the first animal was born. Another step toward complexity is illustrated by the possible presence of colonial organisms. By remaining attached to each other after mitosis, cells achieved an arrangement that opened the door to specialization and differentiation and thus to multicellular organisms.

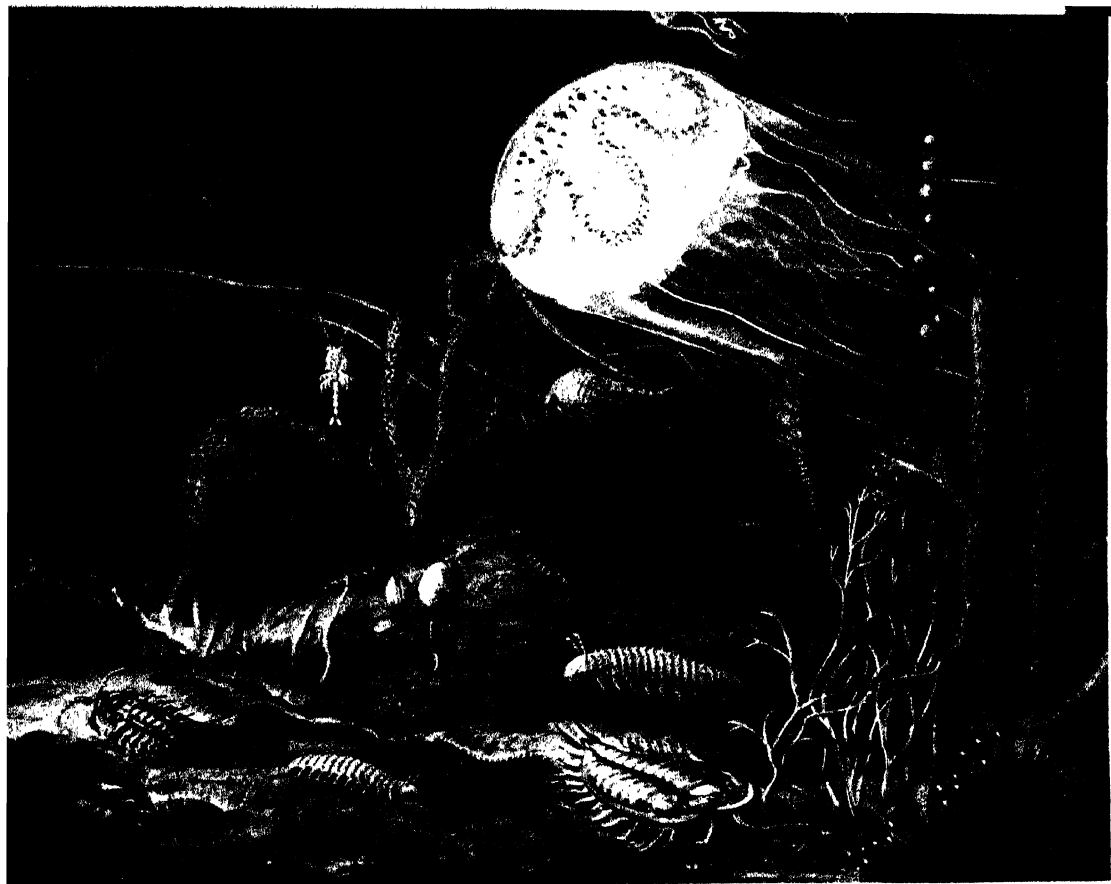


PROTEROZOIC ERA (Vol. 9 to Vol. 15, p. 500)

This was a period of vast sedimentation and the slow grinding down of mountain ranges previously produced by diastrophic action. During the period, new mountain-building rejuvenated the landscape, to be followed once more by a long period of erosion, and finally a second epoch of mountain-building.

Life was still confined to water. The land was desolate. There was no soil, since soil is a product of living organisms. But there was much activity under water. Though living forms were probably too delicate to leave fossils in abundance, certain deductions based

on creatures living today, together with deposits of oil, iron ores, a few sponge spicules, and worm trails, combine to produce a picture. They were probably small jelly fishes, polyps, some worms, and sponges. Under a magnifying glass might have been seen forms similar to those of the earlier era, but specialization among the single-celled animals had probably gone a good deal further. Colonial organization was probably well represented. These are the highest forms of life at the end of the Proterozoic Era — with almost three-fourths of organic evolution-time already past.



Algae	Primitive sponges	Lingula (a brachiopod)	Jellyfish	Stalked cystoid (echinoderm)	Various sponges
Trilobite	Aysheaia (a transitional "worm")	Sidneyia	Aysheaia Trilobite		

PALEOZOIC ERA: CAMBRIAN PERIOD (Vol. 15, p. 501 to Vol. 16, p. 400)

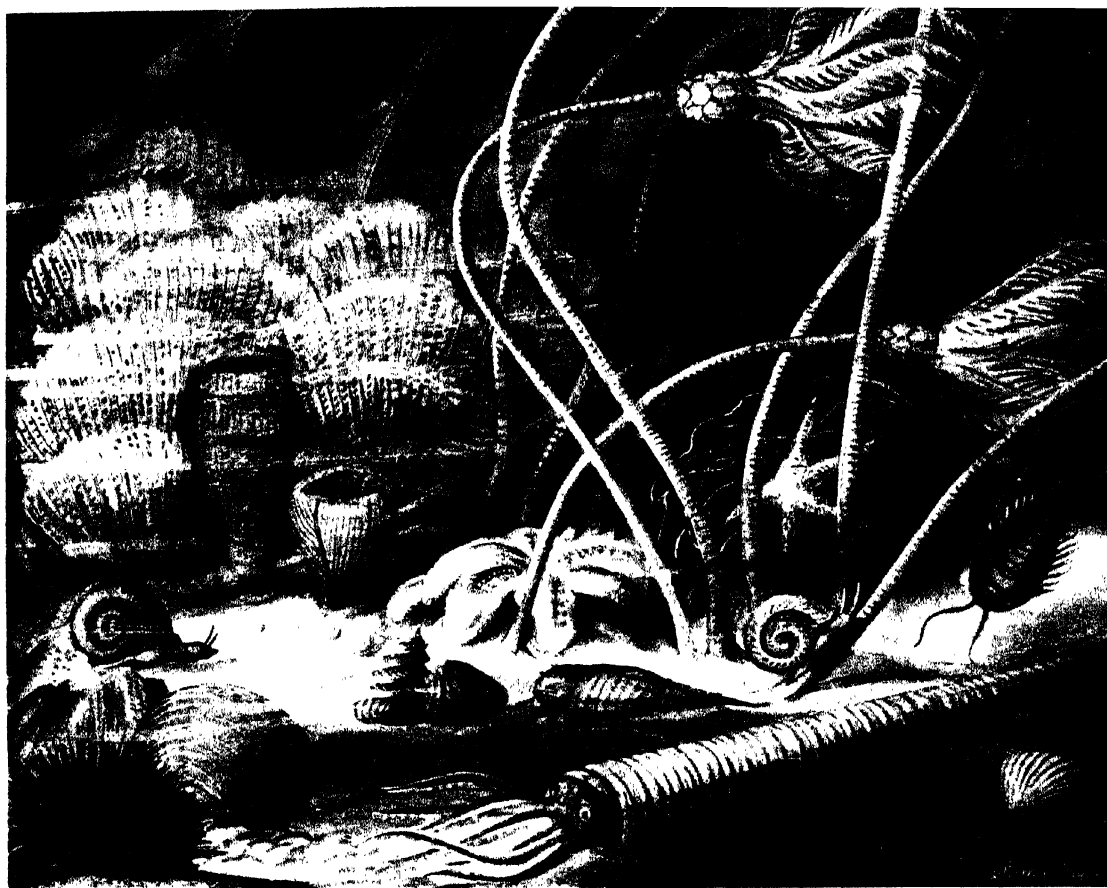
Life in the Cambrian was still limited to the water, but fossils of this period are abundant. The trilobites, which looked much like giant sowbugs, were now dominant forms, and continued to be so for over a hundred million years. Already some of the more progressive ones had begun to evolve into a peculiar creature (*Sidneyia*) resembling the sea scorpions, the eurypterids, which were to become dominating monsters in following periods.

The brachiopods, an isolated class of obscure origin but superficially resembling clams, first appeared in this period. Equipped with dorso-ventrally¹ paired shells, in contrast with the

lateral ones of mollusks, they appear to have lived in enormous numbers, especially in later periods, and today serve the paleontologist as time markers. Primitive forms have hingeless shells, and it is this type that first appeared in the Cambrian. The *Lingula* ("little tongue") of today is a primitive hingeless brachiopod that has come down almost unchanged.

Various echinoderms, early cousins of the starfishes and sea lilies, also had become established. Among the lower metazoans, coelenterates were represented. Surprisingly, even the jellyfishes, which belong to this group, have left fossil imprints. In this period also lived the earliest mollusks, forerunners of modern snails, oysters, and clams. All these organisms appear in crude and "experimental" forms.

¹ *Dorsal* — of or on the back; *ventral* — of or on the front or belly.



Gastropod Corals Astylospongia Eurypterid Sea lilies (crinoids) Gastropod Trilobite
 Sea urchin Brachiopod Gastropod Orthoceras (nautiloid) Brachiopod

PALEOZOIC ERA: ORDOVICIAN PERIOD (Vol. 16, p. 401 to Vol. 17, p. 150)

The Ordovician was a time of great land submergence, but this had little effect on the distribution of life, since the land was still almost barren. Life beneath the sea, however, was quite varied, as the range and structure of all the earlier tribes became much greater, and as new forms evolved. Among the coelenterates, corals made their appearance. The starfishes and their relatives showed an enormous diversification, as did the brachiopods. The shells of snails acquired their characteristic coiling, a considerable improvement over the cumbersome long shells of their ancestors. Bivalve mollusks, and their more distant relatives, the nautiloids, came on the scene. These were the ancestors of the pearly nautilus of today (the "chambered nautilus" of Holmes'

poem), but with a straight shell instead of the present gracefully coiled one.

Among the arthropods, there were new trilobites, and the sea scorpions, the eurypterids, increased greatly in size and adaptive variation. These scorpions were the first representatives of the immensely varied land life to come, but those of this period were still imperfectly adapted to life on land.

Of great importance was the appearance of the first backboned animals, the vertebrates, the group to which mankind belongs. Only fragmentary fossils testify to the existence of vertebrates in this period, but these show that the first vertebrates were fish-like limbless creatures, the ostracoderms, allied to the modern limbless lampreys and hagfishes.



Algae		Algae	Ostracoderm	Crinoid Eurypterid	Blastoid (echinoderm)
Nautiloid	Starfish			Ammonoid	Trilobite
				Ostracoderm (head)	

PALEOZOIC ERA: SILURIAN PERIOD (Vol. 17, p. 151 to p. 500)

Another 35 million years (another 350 pages in our encyclopedia) brings the last phase of the Silurian, and so many things had now happened that it is difficult to say which was most important. A great phase of world-wide mountain building had led to a restriction in the extent of the oceans and a great diversity in land climates. The immensely exacting transition from the water plants to the first land plants had taken place, and animals followed close upon the plants. Scorpions had now definitely established themselves on land, though many probably remained amphibious for a while.

Perhaps equally important was the evolution of more complex animals beneath the water. Eurypterids, now twelve-foot monsters, probably greatly influenced the development of the early vertebrates that shared their environment. Also in this period, a new form of cephalopods ("head — feet"), the ammonoids,

branched off from the nautiloid stock and developed, in later periods, to astonishing proportions, some of them reaching lengths of twenty or thirty feet.

Among the vertebrates, fossils of this age permit us a first good look at the ostracoderms, only fragments of which appeared in the previous period. Though generally similar to the primitive fishes (the cyclostomes) of today, and lacking jaws and teeth, they were heavily armored and would probably not otherwise have survived alongside their terrible contemporaries, the eurypterids. Though primitive, they clearly showed the basic vertebrate pattern. Fragments of other fishes suggest that somewhere in the upper reaches of bodies of fresh water, another group was on the way to developing jaws. But since such regions do not produce good fossils, knowledge of them is fragmentary and extremely shadowy at the best.



Ferns
Club mosses and Horsetails
Algae Corals Eusthenopteron
Dinichthys, an arthropod

(lobe-finned fish) Climatius Cystoid
Corals Primitive shark (echinoderm)
Brachiopods Osteolepis

PALEOZOIC ERA: DEVONIAN PERIOD (Vol. 17, p. 151 to Vol. 18, p. 150)

The end of the Silurian had seen great uplifting disturbances, culminating in widespread mountain building. The increased continental area brought with it a great diversity of climate and widespread aridity. Thus by the close of the Devonian, fifty million years later, the scene on land had changed amazingly. At least along the water's edge, forests of strange new plants clothed the once barren land. Gigantic ferns and club mosses, interspersed with towering horsetails — ancestors of the modest ones now often found along railroad embankments — made up the Devonian forests. As yet there were no flowers, but the earliest seed-bearing plants, the seed ferns, may have been scattered among the spore-bearers. Centipedes, spiders, and primitive insects — simple ancestors of one of the most successful of all animal groups — had already appeared, and

the amazing relationship between insects and plants, today exemplified by bees and flowers, may have been already in the making.

Vertebrates were numerous. Some fishes, such as the arthropods named *Dinichthys* (Gr. "terrible fish") grew to a length of thirty feet. Primitive shark-like fishes, perhaps similar to those that developed the first jaws and teeth, populated the seas. *Climatius*, a spiny-finned shark, besides the two pairs of appendages of the traditional vertebrate, had five supernumerary pairs. Imagine what future land vertebrates might have looked like had a creature such as this become their common ancestor! Some relatively conservative lobe-finned fishes, such as *Osteolepis*, still swam in the Devonian seas, while descendants of more progressive ones, the first amphibians, moved shoreward.



Giant club mosses
Dragonfly

Keraterpeton (amphibian)

Limulus

Horsetails
Dolichosoma (amphibian)
Anthracosaurus

Giant cockroach

Coal ferns
Giant club mosses

PALEOZOIC ERA: CARBONIFEROUS PERIOD (Vol. 18, p. 151 to p. 750)

This was a time of lowlands, warm and wet. Flourishing forests, slowly inundated and killed, only to be raised enough for new accumulations of vegetation to grow on top of them, were at work forming the coal beds. Giant ferns, club mosses and horsetails, and other relatively primitive plants had primarily their own kind to compete with. Seed ferns and strap-leaved primitive seed-plants were still a minority. Flowering plants had not yet appeared. Insects seem to have flourished in the damp, hot swamps, for there were dragonflies with a two-foot wing-spread and cockroaches three to four inches long. The giant eurypterids lived on, but their less impressive contemporaries of

true spider or scorpion construction were firmly established. And their conservative cousins, the king crabs, which originated in the Silurian, were still prevalent as they are even today. It is not clear what compensating adaptations these possess that their relatives the eurypterids lacked.

This period saw the unchallenged rise of the amphibians and also their decline, as their reptile-like descendants began to compete with them too rigorously. Flat heads with feeble brain development, and weak, clumsy, bowed legs sprawled out sideways, still characterized these first important adventurers on the land.



Horsetails Conifers
Seymouria
Limnoscelus (a stem-reptile)

Diasparactus (early reptile)
Dimetrodon (mammal-like reptile)

Cycads

PALEOZOIC ERA: PERMIAN PERIOD (Vol. 18, p. 751 to p. 1000)

By the end of this period, eighteen of our twenty volumes are accounted for. This is the age of the Appalachian Revolution, of widespread diastrophism, symptoms of which had appeared earlier. The Appalachian Mountains now began their growth, raising with them many thousands of feet of Paleozoic sediments. Radical climatic changes, from steaming swampland to arid desert, followed in many regions, with inevitable consequences to both animals and plants. Insects diversified, but the more rigorous climate favored smaller sizes. Among newcomers were the first land snails. In many places forests were giving way to more open country, and along with the seed ferns and strap-leaved *gymnosperms* (plants with naked seeds) appeared other primitive conifers.

In the Permian, reptiles became dominant,

and already foreshadowed the fantastic diversification that was to make the next periods spectacular. Evolving from the basic or "stem" reptiles, the cotylosaurs such as *Seymouria*, certain mammal-like forms, the pelycosaurs, were, oddly, the dominant reptiles of the period. Only a thin stream of this type was to survive and lead to the later dominant mammals. The reptilian forerunners of the great dinosaurs were still obscure. *Varanops*, a primitive pelycosaur, looked superficially like a modern lizard, and gave little evidence of the remarkable potentialities which eventually produced the mammals. Much more mammal-like in skeleton and teeth were such reptiles as *Dimetrodon*, although these had grotesque spine-supported dorsal sails of unknown function. Among other reptiles appeared *Eumotosaurus*, the first "experimental" turtle.



Conifers Tree fern
Horsetail Cycad
Ornithomimus
(primitive dinosaur)

Kannemeyeria
(herbivorous reptile)

Pteranodons
A phytosaur

Cynognathus

A phytosaur

MESOZOIC ERA: TRIASSIC PERIOD (Vol. 19, p. 1 to p. 450)

This period, beginning about 200 million years ago and lasting for about 45 million years, began the age of dinosaurs. The horsetails, the cycadeoids, the seed ferns, and the primitive conifers were still present, but the transition to modern forms had begun.

The grand success of the reptilian pattern now began to express itself by amazing diversification. *Ichthyosaurus* reverted to marine life, and looked for all the world like a fish or a porpoise; the plesiosaurs resembled a combination of seal and ostrich. The peculiar bipedal locomotion of many reptiles, preserved to this day in their descendants the birds, is displayed by *Ornithomimus*. It was with this creature of moderate size that the "ruling"

reptiles, the archosaurs — including the dinosaurs — first appeared. Buried somewhere in Triassic deposits must lie skeletons of ancestral pterosaurs, the weird flying reptiles that suddenly appeared in the following period.

Cynognathus, a mammal-like reptile called the "dog-jawed," looking like a combination of dog and lizard, lived side by side with surviving stem-reptiles, which became extinct at the end of this period. *Cynognathus* had mammal-like teeth, and his legs were supporting pillars, like those of mammals, rather than lateral paddles like the legs of reptiles. Features of mouth and nose, insuring uninterrupted breathing, suggest that the creature may have evolved a degree of warm-bloodedness.



Pterosaur
Archaeopteryx

Allosaurus

Brontosauri

Stegosaurus

a bird-like
dinosaur

MESOZOIC ERA: JURASSIC PERIOD (Vol. 19, p. 451 to p. 800)

This period, ending a mere 120 million years ago, was the great age of the dinosaurs, those reptilian giants familiar to every school child — *Brontosaurus*, with a length of 80 feet from nose to tail; *Stegosaurus*, contender for honors in brainlessness; *Allosaurus*, one of the overwhelming flesh-eaters, measuring 34 feet from head to tail and standing 14 feet high on his massive bird-like feet. In this period the pterosaurs, the winged reptiles, appeared suddenly out of an unknown evolution. They were represented by numerous small forms no larger than sparrows, looked much like bats, and were possibly warm-blooded. The Jurassic saw their peak development in numbers, although the most impressive of them did not appear until the Cretaceous. Evolving side

by side with these were the first links between the reptiles and birds, *Archaeopteryx* and *Archaeornis*, with reptilian skeletons, teeth, and feathers. In the heyday of the giant reptiles, primitive mammals timidly embarked on the journey that led to man. Insignificant pygmies, their only remains are the delicate fragments of jaws and teeth.

Also at this late date appeared the first fore-runners of the modern bony fishes. These were represented by *Leptolepis dubius*. The ammonites experienced a strange re-blossoming. Certain archaic plants, such as the seed-ferns, were slowly waning, while more modern plants increased in number and kind. The period foreshadowed, rather than actually produced, change.



Protoceratops

Tyrannosaurus

Corythosaurus (duck-billed)
Triceratops

Pteranodon

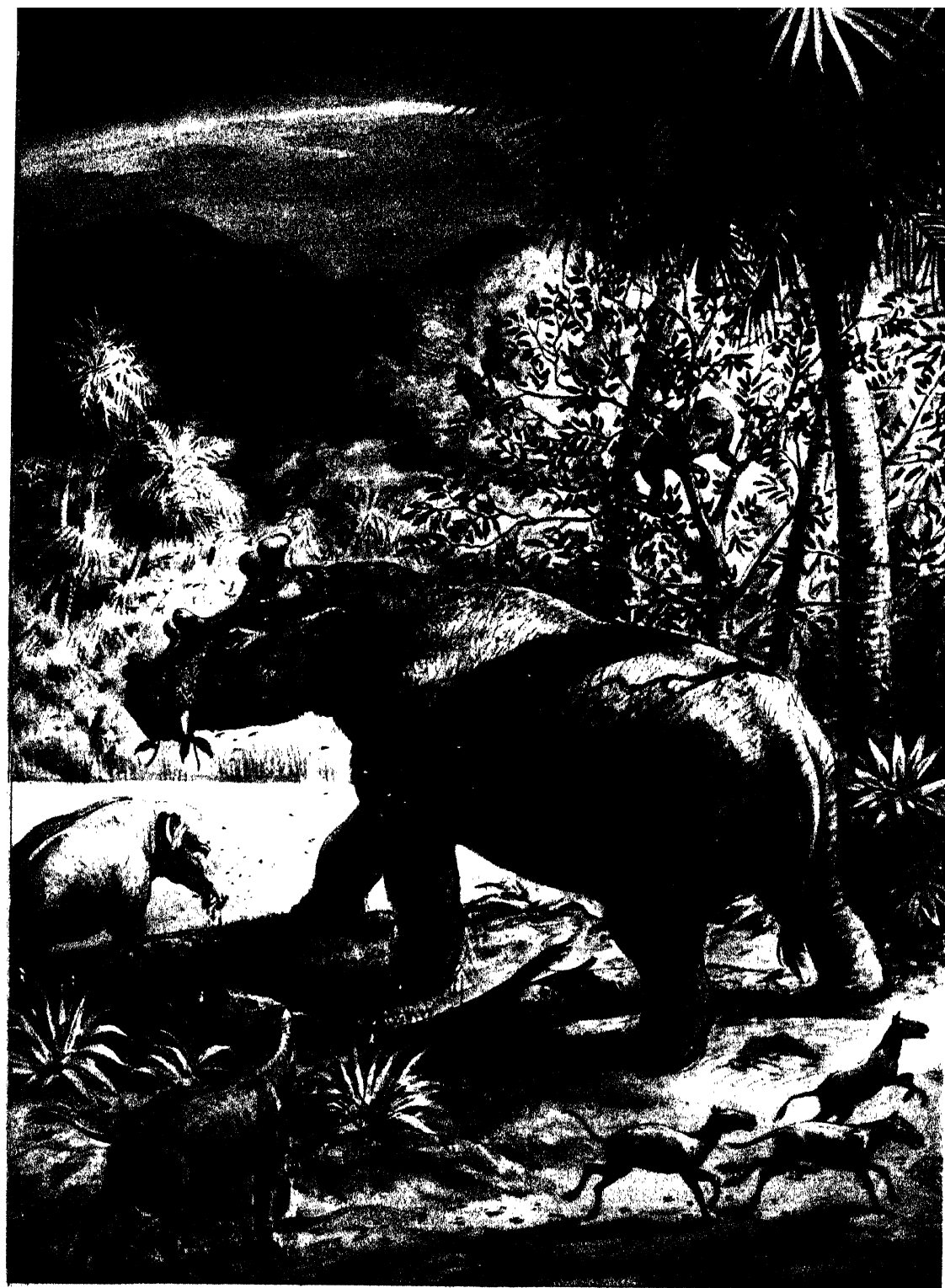
The Cretaceous, marking the end of the Mesozoic Era, was another period climaxed by profound diastrophisms such as the Rocky Mountain Revolution. As in the earlier Appalachian Revolution, former ocean bottoms were raised many thousands of feet as land masses shifted once again and continents once more replaced oceans. These great upheavals resulted in climatic changes, and many regions became colder and dryer, thus shaping the nature and form of evolving life. "Recent" time — the Cenozoic — begins when this period ends, and only half of one volume of our encyclopedia is left to record the rest of history.

The Cretaceous records the dawning of a new world of life, the modern world. Among the fishes, shark-like forms spread and diversified, and primitive teleosts, representatives of modern bony fishes, replaced more primitive forms. Among the amphibians, the first salamanders appeared, and ancestral frogs began to show their specialized and degenerative features. The period witnessed the climax and wane of the great reptilian dinosaurs. Marine lizards, the mosasaurs, reached a length of thirty feet. *Trachodon*, a grotesque duck-billed dinosaur, splashed in the great swamps. Terrible carnivorous dinosaurs, such as the towering twenty-foot *Tyrannosaurus*, encouraged the evolution of fantastic spiked armor on its prey, especially on such tank-like herbivorous forms as *Triceratops* and *Ankylosaurus*, both of which attained a length of twenty feet. But the armor of these creatures appears to have been as desperately futile as the Maginot Line.

More toothed birds made their appearance at this time, modern in most features except the retention of teeth. Many highly specialized forms were already present at this time, among them the tern-like *Ichthyornis* and the very different loon-like *Hesperornis*. Pouched mammals, or marsupials, represented today by such creatures as the American opossum and the

kangaroo of Australia, had spread from their North American homeland over Asia to Australia and southward to South America. They flourished, and would then have seemed to hold more promise than the parallel branch of mammalian evolution, the placental mammals, which soon out-ranked them in intelligence and efficiency, and which were ultimately to supersede them. Even so, placental mammals — and all of the most highly developed modern mammals are of this kind — had begun their first diversification, as had the reptiles and the amphibians, the dominant groups before them. In the Cretaceous Period Australia, stocked with primitive marsupials, became an island-continent isolated from the rest of the world, and thus in the marsupials preserved a form of life which was not equal to the competition offered by the placentals upon other continents, a form of life which otherwise would probably be all but extinct today. Interestingly enough the same thing would have happened in South America, had not this continent become rejoined to North America at a later period, thus opening a path for the invasion of placental mammals from the north.

Practically absent at the beginning of the period, flowering plants — the most successful, various, and highly evolved of all plants living today — became established before its end, and side by side with archaic forms appeared such modern types as plane trees, magnolias, and oaks. Here also began that intimate association between many flowering plants and insects (today most notably the honeybee). At first this relationship was probably casual, but today it has become so highly specialized that many plants depend for their survival upon a single species of insect, and vice versa. The world of life was rapidly assuming its modern aspect, and many of the familiar forms of the present age were being shadowed forth.



Primitive
elephant

Hyrachyus (running
rhinoceros)

Uintatherium

Tarsoid
Eohippus

Throughout this era, initially warm climates gradually became cooler as mountain building continued, with the rise of the Alps and the Himalayas extending into the Miocene. Such climatic changes may have been responsible for the extraordinarily swift rise of the angiosperms, the flowering plants, though these may not have arisen as swiftly as geological records seem to indicate and may have had a longer period of evolution at the end of the Mesozoic, unrecorded because of their upland habits. At any rate, the appearance of herbaceous flowering plants and grasses (*monocotyledons*) brought about a change in the landscape as forests gave way to open, grassy plains. The swiftly growing, swiftly maturing annual plant succeeds in severe climates where larger plants fail. Such climatically induced changes in the flora were bound to have marked effects on the form and variety of animal life.

Dinosaurs, in all their impressive size and variety, had disappeared, and perhaps the climatic disturbances caused by such events as the building of the Rocky Mountains and the Andes had contributed to their decline.

In the Eocene, with startling abruptness, mammals with a vaguely modern look lacking in definite modern characteristics, began to appear. Carnivorous and herbivorous mammals were already markedly differentiated, though both were probably descended from the insignificant insect-eating mammalian pioneers of the late Triassic. Primitive carnivorous creodonts (gr. *kréas* = flesh + *odous* = tooth) like *Oxyaena*, built like a clumsy giant weasel, appear to have existed alongside the miacids, the larger-brained great-grand-fathers of the large tribe of modern bears, dogs, cats, weasels, and walruses. These early ancestors of modern carnivores were also called fissipedes ("split-feet") and are represented by such forms as *Cynodictis*. *Eohippus*, the dawn-horse, was at the beginning of his career. The fact that carnivores killed off many of the less fleet-footed animals was to result in

an amazing increase in size and speed, even as the development of escape techniques by the herbivores called for ever-increasing efficiency and intelligence in the predators. Thus the slow-witted creodonts passed out of the picture as the slow and stupid herbivores of their time were replaced by the fleet-footed and more intelligent hoofed animals. *Hyrachyus*, the running rhinoceros, looked more like a modern horse than did *Eohippus* or the primitive *Phenacodus*, once thought to be the ancestor of many hoofed animals. In his primitive structure, *Phenacodus* preserves the pattern of such a common ancestor. Noteworthy for size and uncouth appearance were the amblypods, represented by *Uintatherium*, as large as a modern rhinoceros.

The first recognizable ancestors of the sea cows and manatees appeared, the only purely marine orders of mammals. Somewhere along the African coast of the Mediterranean, the shore-dwelling ancestors of whales started their irreversible journey back into the water. In Africa too, there had evolved primitive proboscideans, descendants of still more primitive ungulate stock, and ancestors of the modern elephant. Marsupials were numerous and considerably varied.

Bats appeared, already fully evolved, with much the same flight technique as the ancient flying reptiles. Rodents established themselves. Perhaps most important of all, from the human standpoint, we find teeth and parts of the jaws of small mammals which suggest that these were ancestral forms of such modern primates as the lemurs and *Tarsius*, and perhaps also of monkeys, apes, and man. These tree-dwelling insectivores, our probable ancestral relatives, may be pictured as small lemur-like creatures, while others may have approached *Tarsius* in appearance. In any event, it appears likely that our ancestors at this time were more or less rat-sized, and superficially rat-like, tree dwellers. No prophet could have guessed their future.



Archaeotherium
(a "giant pig")

Titanotherium

Shrews (insectivores)

Propliopithecus (?)
Baluchitherium
Meshippus

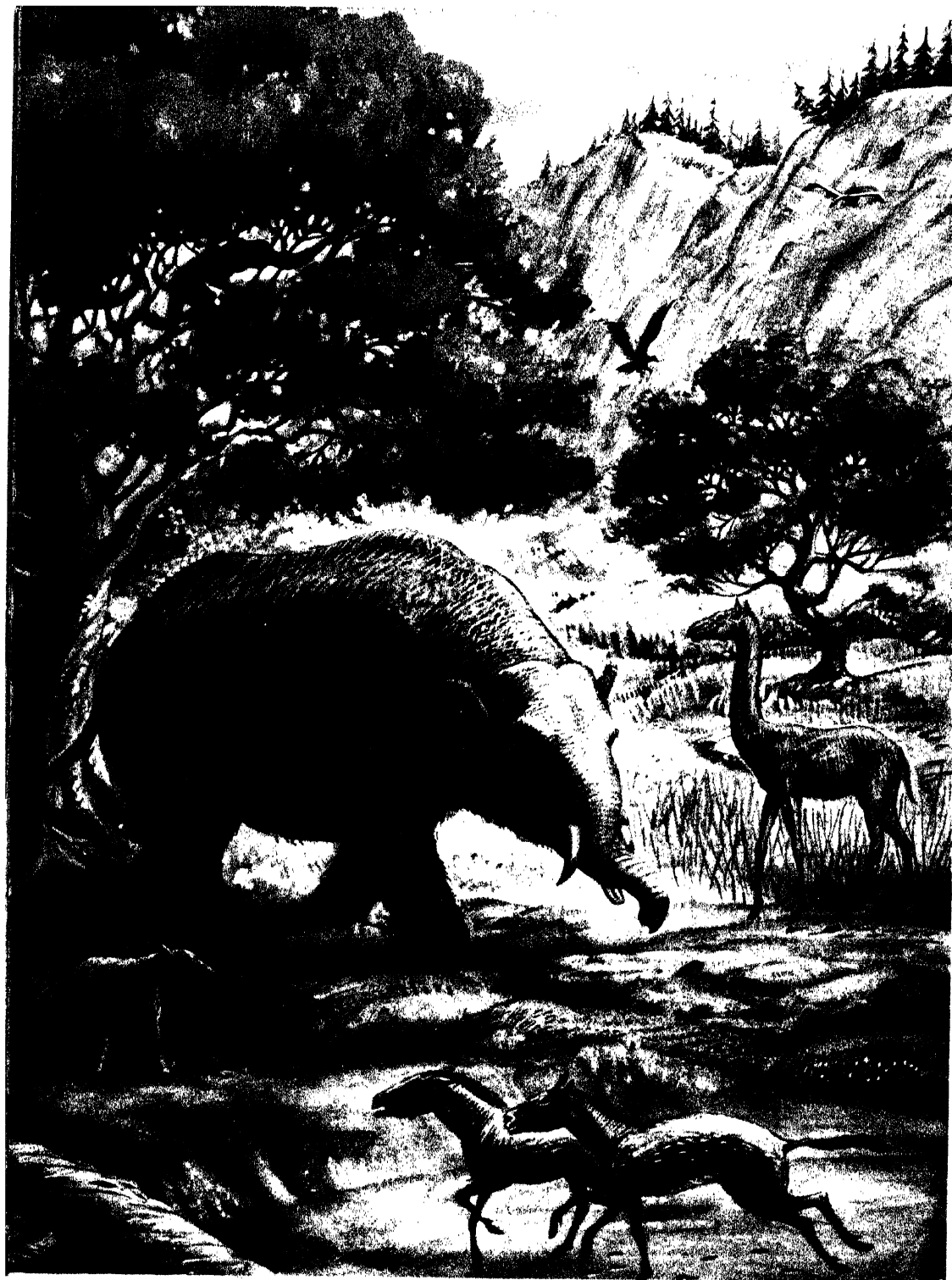
CENOZOIC ERA: OLIGOCENE PERIOD (Vol. 20, p. 651 to p. 800)

The next fifteen million years, covered by the Oligocene period, brought a diversification of the mammals similar to the explosive diversification of the reptiles in the period of their dominance. There were many primitive forms of modern mammals, though these may be considered as archaic mammals that eventually failed to adapt to a changing environment and thus became extinct, rather than as direct ancestors of existing modern forms. The unbelievable *Baluchitherium*, a sort of rhinoceros eighteen feet high at the shoulder, is a relic of this epoch. The titanotheres (titanic beasts) were abundant in the Americas at this time but later abruptly disappeared. Though they were armed with horns and attained the bulk of elephants, the weakness which led to their extermination may have been their teeth, which were constructed for lush plant foods, so that climatic changes that influenced the type of flora available to them as food may have caused their disappearance. There was a great spreading of primitive ruminants, cud-chewing animals, and in North America their fossil remains outnumber those of all other mammals combined. It is from these somewhat pig-like creatures, and from similar forms, that later ruminants such as camels, cattle, and others arose. *Mesohippus*, a primitive horse, has now reached the size of a collic, and *Miohippus* even exceeds it in size. Both now have three toes, the central toe however definitely enlarged and elongated, and bearing the brunt of the animal's weight. The modern one-toed horse is clearly foreshadowed. Miocids

abound at the beginning of the period, but their progressive fissiped descendants become dominant towards its close, gradually replacing them. The probable ancestor of the dog, the mink-sized *Cynodictis*, was also the ancestral form of most other modern carnivores. Both dog-like and cat-like features appeared in the peculiar generalized design of this creature. The Oligocene also produced the famous saber-toothed cats, which appear to have evolved their weapons at about the time the thick-hided giant plant-eaters of the epoch developed their armor. Primitive proboscidsians, ancestors of modern elephants, looked much like the "elephant's child" of Kipling before the alligator stretched his nose into a trunk.

Pigs appeared on the scene, and primitive beavers. Porcupines, possibly of African origin, suddenly became abundant in South America, and their invasion presents an unsolved mystery. In the water there were early sea cows, and the whales had begun their diversification. Marsupials were still present in South America, and some of the carnivorous forms had evolved to the size of bears.

The faint — though increasingly distinct — thread of human evolution appears in the form of a jaw no larger than that of a small monkey. The animal represented by this significant remnant is known as *Propliopithecus* and was the ancestor of modern gibbons and perhaps of the great apes and man. We may assume that this creature had much the general appearance of the modern gibbon but was less highly specialized.



Primitive Dog

Pliopithecus (?)

Trilophodon

Merychippus

Alticamelus ("giraffe-camel")

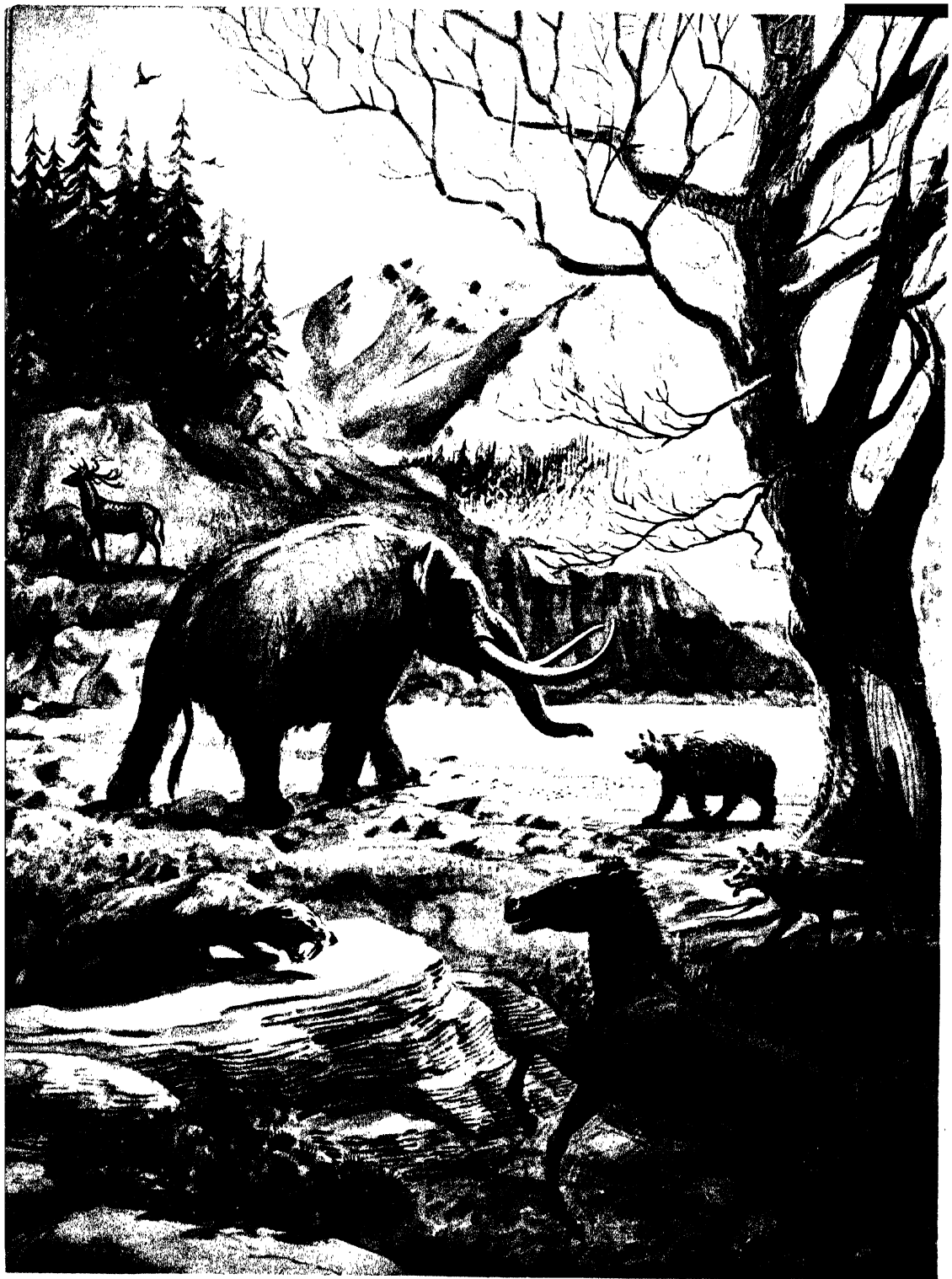
CENOZOIC ERA: MIOCENE PERIOD (Vol. 20, p. 801 to p. 920)

During the twelve million years of this period, evolutionary changes do not appear to have been particularly striking or abrupt. Rather, there was a slow but more or less continuous transition from archaic forms to modern ones. Increasing coolness of climate was probably a contributing factor to the gradualness of this process. The note of modernity becomes clear and unmistakable in this period. Half of the present living fauna were already represented. There were various dogs and early bears and the saber-toothed cats had become even more terrible than in the preceding period. Archaic types were disappearing, especially among the ungulates or hoofed animals. The horse was represented by *Merychippus*, which was about half as large as the modern horse and now walked on single toes as does its modern descendant.

But the plains of North America presented a strange picture, for here roamed the rhinoceros and tapir together with ancestral horses, represented not only by *Merychippus*, but by more primitive types as well. Herds of varied camels added to the strangeness of the scene. In Europe, deer-like forms had evolved, and primitive antelopes as well as giraffe-like forms appeared in Eurasia. Towards the end of the period, the four-tusked Mastodon, *Trilophodon*, found its way to America, and rabbits and rats were common everywhere, then as now. In the water, whales were flourishing as never before or since, and almost all families still in existence today were then present, as well as many now extinct. And those strange half water- half land-creatures, the seals and walruses, had appeared.

South American marsupials had developed and flourished as a result of their Eocene separation from the North American continent. In South America, the absence of placental carnivores permitted the rise of marsupial carnivores. The outward similarity achieved by these two distantly related groups of carnivores, under the stimulus of a similar, special type of selective environmental influence, is astonishing. As marine life produced the porpoise (a mammal), the shark (a fish), and the ichthyosaur (a reptile), each with the same "hull," so certain marsupials evolved into dog-like and cat-like carnivores. Thus the placental cats had a marsupial duplicate in *Borhyaena*, a puma-like animal. More or less dog-like in appearance was *Prothylacinus*. The odd rabbit-like ungulate, *Protypotherium*, was not what it superficially appeared to be, for in spite of externals, it bore no close relationship to the rabbit.

Finally, the human trail reveals an ancestral gibbon, *Pliopithecus*, and tantalizing fragmentary remains of a great ape, *Dryopithecus*. *Dryopithecus* was definitely ape, not man, but his jaws and teeth suggest that he may still have been close to the common ancestral line that produced not only modern apes but man as well. We may picture it, perhaps, as a creature something like the modern gorilla, but more generalized and less highly specialized. At about this time, if not earlier, the line of human evolution must have branched off from that of the modern great apes, each to follow its own course of development. By this time the trail that leads to man grows slightly clearer.



Deer-like ruminants
Saber-toothed cat

Mastodon

Bear
Horse

Dog

CENOZOIC ERA: PLIOCENE PERIOD (Vol. 20, p. 921 to p. 990)

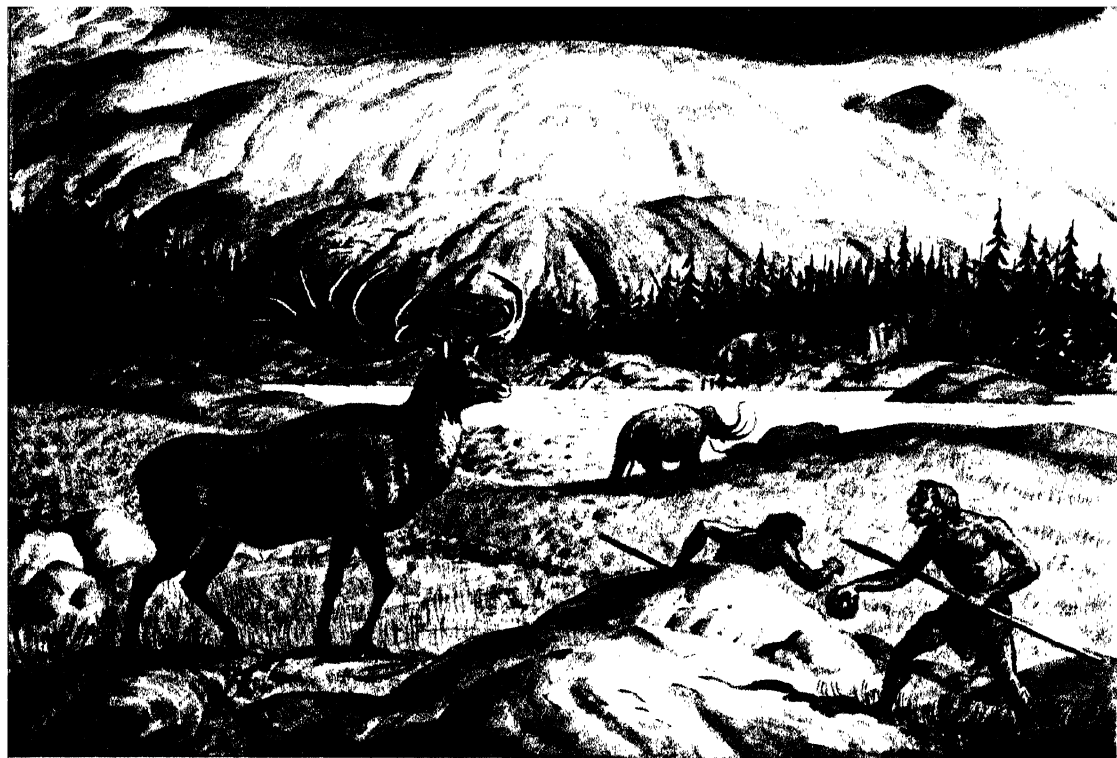
At the end of this period (a brief seven million years), but ten pages remain of our twenty volumes. Increasing coolness of climate continued, and helped to shape the pattern of plant and animal life. The hoofed animals had prospered and produced many divergent forms in response to the changing plant world, but many old families had gone. Horses were abundant, including such types as *Pliohippus*, from which descended the modern horse. Although camels still flourished, North America had no bovids — the cattle, sheep, and goats. Dry, open plains and the grassy plants they grew favored the highly specialized digestive system of the cud-chewers or ruminants. By virtue of their complex stomachs, deer, goats, cows, and others could quickly bolt large quantities of food, to be regurgitated later and thoroughly chewed in safety.

Bovids, all ruminants, were abundant in Eurasia and later in Africa. Indeed, Africa was later to become a haven for such refugees from the advancing cold, and the Eurasian fauna of this period was much like the African fauna of today. The bovids are considered the most successful of the ungulates, but as latecomers, their migration to North America was sparse, hindered perhaps by the very lateness of their appearance, at a time just preceding the increasing cold of the Pleistocene, when the Si-

beria-Alaska bridge had already become a difficult passage. Thus only northern types of Bovids ever invaded the Americas, and none ever reached South America.

The mastodon, a relative of the modern elephant, roamed over the Americas, and together with another relative, the mammoth, probably persisted until a few thousand years ago. Bears, such as *Hyaenarctos*, were now distinct from their dog-like ancestors. Dogs, foxes, wolves, and hyenas had appeared, as had seals, whales, and many other modern forms. Indeed, the fauna had a remarkably modern aspect, and fully 80 per cent of the terrestrial families then present have survived to the present. In South America, marsupials still ruled, and effective carnivores had sprung from their ranks, even to evolving marsupial saber-teeth, indeed a remarkable instance of parallel evolution. But the great migration of North American placentals into South America had begun, and the indigenous marsupials, no match for these superior invaders, faced rapid extinction.

Our picture of the primates of the Pliocene — the line leading to man — is fragmentary at best. Scattered remains of *Dryopithecus* (teeth of the upper cheek and most of the lower jaw) give some notion of man's possible ancestors or close relatives.



Above: Megaceros (giant elk)
Below: Megatherium (giant sloth)

Mastodon

Pithecanthropus
Glyptodon

At the end of this period, extending from about a million years ago to some 30,000 years ago, we are well down the last page of our encyclopedia. The world had become increasingly cold, and at the beginning of the Pleistocene the polar ice caps reached out toward the equator while the glaciers of the southern mountain valleys crept down to meet them. The great Ice Age which had now begun was not continuous, however, but came in two periods of two waves each. The glaciations within a period were separated by a brief span of mildness, while the two main periods themselves were separated by a long interglacial interval. As the ice came, tundras formed, and deserts such as the Sahara and that of the southwestern United States were well watered.

Among creatures caught in the wintry vise, only the strong and the highly adaptable could survive, while new types adapted to cold and bleakness evolved. The horses weathered the change, and camels roamed their American homeland. But many forms, and frequently the larger ones, became extinct, either as a direct result of the glacial period or for other reasons. Among these was the American mastodon, survived by the elephant, and the

saber-toothed cats, contemporaries of early man. One fantastic creature of the period was the giant *Glyptodon*, a relative of the modern armadillo, but reaching a length of ten feet.

Impressive in its massive stupidity was the giant ground sloth, *Megatherium*, twenty feet long. The giant elk, *Megaceros*, was as large as a horse and burdened with unbelievable antlers. All of these are now extinct, and we can but guess at the imbalance or lack of adaptability that led to their disappearance. Magnificent specialization and giant bulk were no guarantee of survival.

The Pleistocene saw the dawn of man, and this of course for us outshines in interest most other events of the period. There were man-like off-shoots of the primate line, such as the *Australopithecus* of South Africa, and possibly giant ape-men in Java, such as the *Meganthropus* and *Gigantopithecus*, as suggested by Weidenreich. But there were also definite man-like types, especially the Asiatic *Pithecanthropus*, an offshoot from the main line of human evolution thought to have been an ancestor of the Australian aborigines of today, and perhaps of other human stocks as well. *Pithecanthropus* is considered distinctly human.

CENOZOIC ERA: THE RECENT PERIOD (Vol. 20, last 15 lines)

The Recent Period, which first saw modern man, *Homo sapiens* ("man the knowing"), dates back 30,000 years—but a moment in the evolution of life, vast as the period may seem compared to our fleeting individual lives. By the beginning of this epoch—perhaps much earlier—man had reached the form he has today—which by no means implies that he has reached a "goal." His evolution has not ended. The human form of today may be merely another step in the evolution of a being probably as far beyond our present state as we are beyond the amoeba. Or the future may reveal flaws in human adaptability so great that man too will follow

the countless former rulers of the earth into extinction and oblivion. Man's control over his environment, made possible by the enormous specialization of his brain, the organ which makes him the most adaptable animal of all time, promises to give him control of the world until the world ceases to be. His lack of specialization in other respects also promises well for his chances of survival. But his failure as a social animal to keep pace with his ability as a clever manipulator of matter may bring about his extinction. The story is being written, and whoever reads it now must be reconciled to the fact that he will never live to read the final chapter.

The Mechanism of Evolution

THREE THEORIES

Now that we have seen something of the immense diversity of life, and the countless varieties of living things which have evolved, changed, and survived, or declined and become extinct, it may be asked how and by what mechanism all this lavish diversity came about, and what pattern, if any, is determinable in it. In doing so we may begin with a brief examination of the principal theories which evolutionary thinkers have advanced from time to time, beginning with two that are no longer widely held but once had a wide appeal, partly because they gave a comforting sense of order, direction, and purpose — but a false simplicity — to the facts now known.

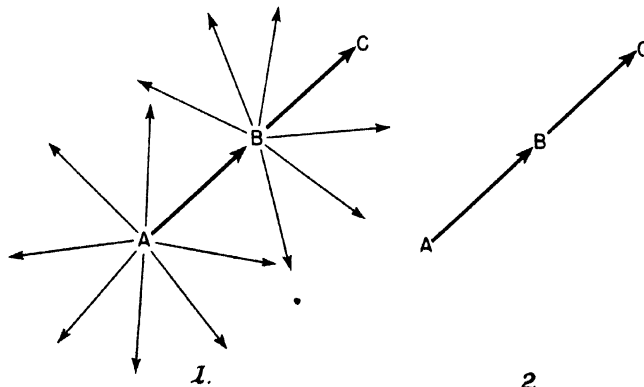
That organisms possess characteristics which adapt them to their environment is common knowledge. It is equally clear, from the many varieties of domestic animals and plants that now exist, that they change. It was long thought that such changes and adaptations were due either to a directional drive within the organism which caused mutations to follow

a definite pattern, or to the influence of environment on previous generations. Since both these theories have been widely held, it is worth while to examine them briefly before considering the hypothesis now generally accepted.

Orthogenesis

The first of these beliefs was known as the principle of orthogenesis ("straight beginnings"). According to this theory it was thought that organisms tended to change in a given direction, that mutations did not occur at random, but were directional and thus gave rise to a straight line of evolution according to some predetermined course (Fig. 104). The changes in the horse's foot could be, and were, argued as a case of orthogenesis. But this is perhaps not the best example, for while this appendage clearly underwent a series of useful changes, they could conceivably have been brought about by random mutations channeled by the selective effect of environment. Clearer evidence, perhaps, could be seen in such apparently useless structures as the ornate spines

Fig. 104. If *A* is the starting point and random mutations radiate from it (as in 1), one will eventually reach *B*, and from *B* will eventually reach *C*. According to orthogenesis (2) an inner urge would cause the change from *A* to *B* to *C* in a straight line.



and spikes on some of the later ammonites, the over-developed bony fins of certain mammal-like reptiles like *Dimetrodon*, and the exaggerated antlers of the extinct Irish elk.¹ All these structures seem more troublesome than useful to their possessors, and hence may possibly be considered the result of a trend in mutation which persisted regardless of environmental selection. It is even possible that such a trend may have led to the extinction of these species, although the evidence for this is not conclusive, since such a harmful or meaningless feature could have been intimately linked with one of marked survival value. But the innumerable mutations that show no trend, and the many damaging mutations that appear in carefully observed organisms, tend to rule out the theory of orthogenesis as a general explanation of the evolutionary process. Consequently it is not widely accepted today.

Inheritance of Acquired Characteristics

Another belief no longer generally held is that characteristics acquired during the lifetime of an organism can be inherited. The question whether acquired as well as hereditary characteristics may be passed on has long been debated, and while most of the evidence today indicates that they cannot, the battle has been intense and is not yet completely over. The French naturalist, Jean Baptiste Lamarck (1744-1829), first proposed the theory as a basis for evolution, and Darwin supported and attempted to explain it with his *pangene theory*. Darwin did not attribute all changes "of corporeal and mental powers" to those variations which are "often called spontaneous." He clearly stated that great weight must be attributed to the inherited effects of use and disuse with respect both to body and to mind. On the basis of the facts then known, he argued that under the influence of environment, the body cells may produce specific substances which he called *pangenes*. These were supposed to be conveyed to the germ cells by the circulatory system, and in turn to cause corresponding

changes in the bodies of offspring. This is not in itself an unlikely theory. If true, it would account for the classic example of Lamarckian thought — and one of the most obvious illustrations of "acquired" characteristics — that giraffes have long necks because for generations they have reached for leaves on the tops of bushes and trees, and that the longer neck thus produced was passed on in the course of generations to their offspring. At first sight that theory is persuasive, and Darwin's attempt to show the mechanism by which it worked was ingenious. But the facts at our disposal today lend it no support.

Evidence against the theory is of two kinds, the unplanned experiments observable in nature, and the planned ones conducted in the laboratory. Let us first consider a few of the former, from the wealth of those available.

Evidence in Nature. In certain Polynesian races the earlobes of children are pierced, and the punctures are gradually enlarged by the insertion of wooden plugs of increasing size, until the lobe actually hangs down upon the shoulder and a large grapefruit could easily be passed through the opening. The African Ubangis and the Botocudos of South America stretch the lips by means of transverse incisions held open by large wooden plugs (Fig. 105). Certain Semitic peoples have practiced circumcision for perhaps four thousand years. For generations, the feet of Chinese girls were bound in early youth, thus producing dwarfed and deformed "lily feet." These and other mutilations could be expected to leave a mark of some sort on succeeding generations if such a thing were possible, but no evidence of this has ever been found. Finally, the use of one language by generations of his ancestors does not appear to alter the ability of a child of one nationality to grow up as a "native" speaker of another tongue, be it ever so different. Thus the unplanned experiments observable in nature give strong evidence against the inheritance of acquired characteristics.

Experimental Evidence. Planned experiments have ranged from crude physical mutilation, such as docking the tails of mice for

¹ See pages 142 and 143.



Galloway

Fig. 105. Distorted lip-tissues producing the beak-like mouths of Ubangi women. The children show no trace of such beautification.

many generations, to more subtle influences, such as induced alcoholism, defects resulting from the use of antibodies (specific chemicals injected into the blood), and the training of animals. Docking the tails of mice requires no further explanation, and it will hardly be surprising that the young mice were not born with shorter tails. Less clear are the results of experiments with chemical influences. Some animals kept for long periods under the influence of alcohol produced defective offspring; others had fewer offspring but stronger ones, perhaps because only the strongest could survive while the weak failed to develop at all. Even in the defective offspring, the results seemed to disappear after a few generations, so that it is doubtful whether any genes had actually been changed. Even if they had been, it would indicate only that some chemical substances may alter the structure of genes without destroying them completely and would not provide a clear-cut case of inheritance of an acquired characteristic. The great difficulty in evaluating such experiments becomes clear

when we learn that certain heritable changes, apparently brought about by the use of specific toxins, later appeared in untreated stock with sufficient frequency to make the experimental results questionable. Only experiments carried out on highly inbred and hence homozygous (genetically "pure") stock may be expected to produce reliable results. On the whole, the effects of environment do not produce conformable or consonant changes, and except for outright mutations they produce few changes of any kind.

The Present View

What, then, does the evidence show? Again and again it indicates that changes in species are random in nature and that the illusion of pattern and seemingly adaptive mutation is merely the effect of a selective environment which favors certain structures for survival and consigns others to oblivion.

The present view may be illustrated by the use of an analogy. Random mutations may be thought of as being like random inkspots

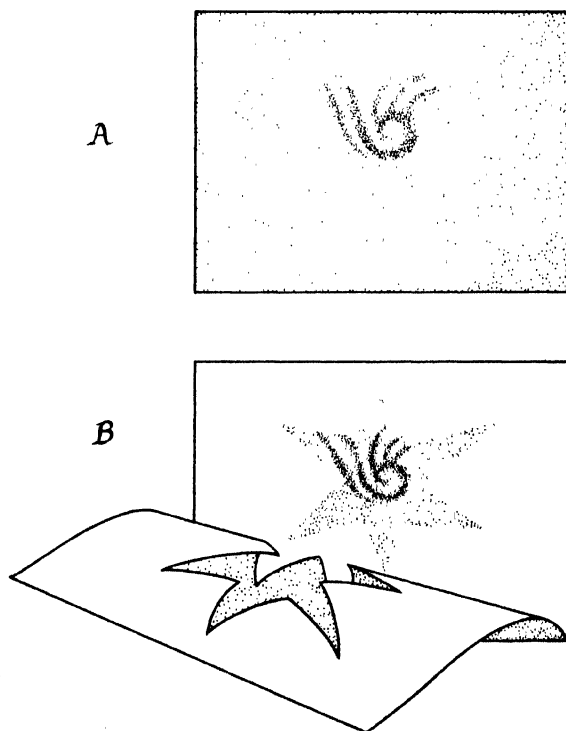
splattered without premeditated design over a blank wall. If a stencil is first placed over the wall, however, only the spots falling within the open area of the stencil will strike the wall, for the stencil will block all the others (Fig. 106). Thus the random splatterings which reach the wall conform perfectly to the shape of the stencil, so that the sprayed pattern thus produced fits into this particular stencil with absolute precision. Air currents or other environmental variables may prevent the spatter pattern from being absolutely uniform, or the droplets may even be blown aside entirely from various regions, leaving them blank, while others are crowded more densely.

How does this analogy apply to the problem of evolution? The environment, acting as a stencil, selects those mutations which fall within its pattern and blocks out others which do not. Thus while mutations may occur at random over an extremely wide range of possibilities, only those are preserved which maintain or improve the chances of the organism to survive within its environment. All existing studies of the nature of mutations show that they are random in so far as functional relationship to the environment is concerned; that is, they follow no trend, either "beneficial" or "harmful." And the environmental stencil exerts no directional influence on the splattering drop. Certain random mutations happen to increase the organism's effectiveness in its environment, and these tend to be preserved — they are within the stencil.

Though there is no indication that mutations in any way occur in response to the demands of the environment, there are, of course, limits within which any given gene may be expected to change. Thus mutation is definitely restricted by the existing chemical form of the gene, and each gene can mutate only in a few ways — perhaps ten or twenty or even less. Hence mutations are not random in the sense that a gene can mutate in a limitless number of ways. Furthermore, the chemical structure of a gene, like that of any other molecule, will give it a greater instability in one direction than in another. Thus certain mutations arise re-

peatedly, and gene-determined traits may exhibit a certain directional trend in their mutations, which, however, generally bear no visible functional relationship to the demands of the environment. Thus there is a pattern in evolution, but not one imposed by an urge inherent within the organism, nor one fostered by acquired traits which carry over to new generations. The trend is more likely to carry the organism completely out of the environmental stencil to extinction than it is to follow the pattern laid down by the stencil. This, as we have seen, happened repeatedly in ages past. Yet the very existence of the stencil often gives the appearance of a pattern to the development of those organisms whose mutations have been favorable to survival within the environment. Let us now look more closely at the details of the mechanism by which all this takes place.

Fig. 106. Stencil effect of environment on random mutations. Spiral design in splattering suggests that an inherent trend may appear within the bolder pattern of the environmental stencil.



THE FOUR DIRECTIVE FACTORS IN EVOLUTION

Four main factors appear to operate in the evolutionary process. These are *heredity*, which endows the species with basic stability from generation to generation; *variation*, which produces the spontaneous appearance of new forms different from the parent stock; *selection*, which results in successful survival or decimation and probably ultimate extermination, depending upon the adaptability of the organism to its environment; and *isolation*, by which some forms are separated from others so that cross breeding is prevented and the differences between populations and species are maintained.

Heredity

Order in the world of life would be impossible without great stability of the hereditary units from generation to generation, and this stability inheres in the genes, the conveyors of hereditary characteristics, collectively referred to as the germ plasm. According to one theory, the germ plasm may be considered the essential stream of life, and the body in which it is housed may be looked upon as merely incidental to its existence. This idea, first stated by August Weismann, a nineteenth century German biologist, suggested that the germ plasm represents an immortal continuum, handed down since the beginning of life from generation to generation. Whereas previously it has been assumed that the body of an organism produced the germ cells for the next generation, Weismann held that the egg produces the mother but the mother does not produce the egg; rather, the egg is produced from the germ cells which also produced the somatic cells of her body. The only genetic relationship, then, between her body and her germ cells is that both are derived from a common ancestral cell.

Thus an ever widening stream of immortal germ plasm flows through time, branching as it goes, evolving change after change, though most of these changes are expressed only in

ephemeral somatic structures which temporarily house and nourish the vital substance. Life then becomes not the evolution of specialized individuals, but of a self-perpetuating stream.

While not completely substantiated, this is not merely an armchair theory. Mechanisms have been found in certain lower organisms which show a sharp segregation between those cells that will eventually form the reproductive cells and those which will form the rest of the body, and this may occur in some species very early in the life of the embryo. Some investigators believe they have demonstrated a similar mechanism for the isolation of the germ line in higher animals. Others dispute such a sharp separation. The fact remains that germ cells never arise from markedly differentiated body cells, and at most from the mildly modified group of potential germ cells, the germinal epithelium. In short, in animals they do show a remarkable degree of segregation from the body cells which surround them. But in plants the principle has less validity.

The theory of the continuity of the germ plasm, and the evidence which supports it, clearly argue that acquired characteristics are not heritable. The isolated condition of the germ cells within the body would make it unlikely that changes produced in the body of an organism by acquired characteristics would correspondingly affect the germ cells. Influence on the germ cells through chemical agents carried in the body fluids or in the blood would, of course, still be a possibility.

Modern knowledge of the role of chromosomes somewhat alters our concept of this theory, but it remains nonetheless remarkable. It does not conflict with the fact that direct influences on the germ plasm may cause hereditary changes in it. Yet the theory does not solve the problem of the origin of seemingly functional or adaptive mutations. As we have already seen,¹ within the germ cell there is a series of bodies known as chromosomes, small rod-like structures which contain the genes, the actual determiners of heredity. A gene is

¹ See pages 80-85.

an autocatalytic entity capable of initiating or directing specific chemical processes within the cell under certain environmental conditions.¹ It is, in short, the unit determiner of hereditary characteristics. As has been previously stated, the genes display a remarkable stability, each reproducing its own kind for a million cell generations or more without mutating. It is this stability in the genes which provides the basis of heredity.

Variation

But stability means resistance to change, and since there is evolution, the stability of the genes cannot be absolute. Observation has repeatedly shown that the hereditary factors are relatively but not unalterably stable. Another way of saying this is that genes maintain their structure under most conditions but are capable of change, either induced or spontaneous, and that this change or mutation is heritable.

The physical and chemical properties of a molecule are determined by its composition and structure. In some cases, its properties can be drastically changed merely by moving one of its component atoms from one position within the molecule to another. Remember that a molecule of glycerose has the same number of carbon, hydrogen, and oxygen atoms as a molecule of lactic acid ($C_3H_6O_3$). But since these atoms are not arranged in the same manner, the two compounds have very different physical and chemical properties. It would not be surprising, then, to find a gene-molecule as subject to change under the influence of outside forces as any other molecule. Indeed, it is only surprising that it is not so influenced oftener, and that it shows such great stability. It is also remarkable that, having changed in structure, it should retain its powers of reproduction or autocatalysis, and that it may, in rare instances, even be a better structure, from the standpoint of survival, than the one from which it was produced.

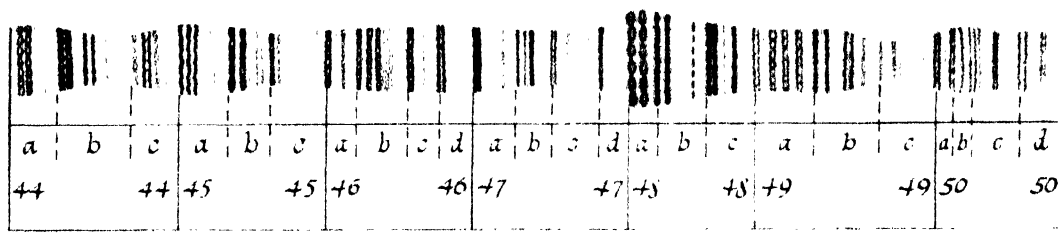
The Rate of Mutations. Although the mutation rates of genes are very low, on the order of one in a million, mutant individuals are far less rare, for a single zygote may be a composite of ten thousand or more genes. Thus we could expect to find a mutant form, though perhaps not one visibly apparent, in one out of every ten individuals. Although the chance that such a mutant will be an improvement over the "normal" stock is slim, the possibility of a better one turning up sooner or later in populations numbering in the thousands of millions is significant.

Induced Mutations. The discovery by Muller in 1927 that X-rays are capable of inducing gene mutations has led to many similar discoveries since, and has fundamentally changed the concept of the nature of genes. Although it had long been known that genes do change or mutate, these changes were referred to as "spontaneous," a rather thinly veiled confession of often unconscious ignorance. Since Muller's work, innumerable artificially induced mutations have been reported from all over the world. And X-rays are by no means unique in their power to change genes. Ultraviolet rays have proved effective, as have many different chemical substances such as mustard gas and nitrogen mustard, ethyl urethane, and colchicine. Methods used generally involved direct exposure of eggs to the chemicals, either by immersion or by injection of the substances into the body cavity. Thus Hadorn in 1946 reported *Drosophila* mutations from gonads removed, treated with phenol, and implanted in new individuals. And Demerec achieved increased mutations in *Drosophila* and in bacteria by the use of a number of chemicals, especially those of carcinogenic (cancer-producing) nature. The frontier of our knowledge is advancing.

Although work of this type yields information not previously available, it does not yet solve the problem of "spontaneous" mutations, for natural radiation and possible chemical influences could not account for more than a small percentage of such mutations. Shocks from increases and decreases in temperature

¹ See page 84.

A



B

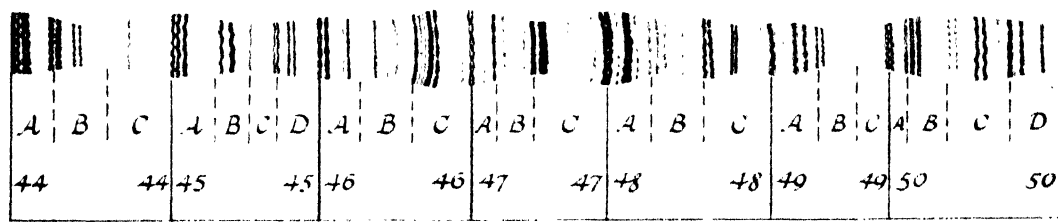


Fig. 107. Maps of the central regions of corresponding chromosomes of two different strains of the insect *Chironomus*. Note the many similarities, but note also the differences which account for the visible differences of the two strains. It has recently been claimed that genes have been seen under the electron microscope.

have been shown to produce mutations. It has been suggested that chance momentary accumulations of energy in a single atom, as they are bound to occur in any collection of atoms, may account for some "spontaneous" mutations, for atoms in a medium of a uniform temperature have a certain average energy value, but differences between individual atoms vary constantly. No organisms are immune to "natural" mutations, and none has as yet proved immune to the induction of mutations by various artificial agents. There is no doubt a specific "cause" for every mutation.

If mutations are changes in the molecular structure of genes, and if artificial mutations are merely random changes brought about by molecular alteration in the genes, it is not surprising to find that induced mutations, like "spontaneous" ones, are purely random in relation to the demands of the environment. An obvious if difficult and distant goal of geneti-

cists would be to cause a new desired mutation in some specific direction. Difficult as such a task would appear to be, it is not only a theoretical possibility, but first steps towards its attainment have perhaps been taken. Numerous reversible mutant forms of the pneumonia organism, *Diplococcus pneumoniae*, are known. In recent years, experimental workers have apparently learned to transform one form into another and back again by the use of proper chemical agents. This may signal a new era in the breeding of organisms and may be compared to the planned procedure of the modern synthesizing chemist.

For the present, we may conclude that mutations can be induced by the direct effect of certain physical and chemical agents on the genes or on the chromosomes, but that influences through and by way of the somatic cells — in other words, acquired characteristics — do not appear to be heritable. If they

are not, then the fact that organisms are adapted to their environment must be otherwise explained.¹

Selection

The third factor in the evolutionary process, along with heredity and variation, is selection. Since genes might mutate in innumerable ways, the variety of strange formations that could thus come about would seem to be almost limitless. It is clear that actually there must be factors which limit mutations within certain defined paths of change so as to maintain the adaptive perfection which we actually find. The primary directive factor of evolution is now held to be selection.

As we have seen, it was once believed that organisms evolved along certain pre-determined paths through sequences of adaptive mutations, all of which tended in the same direction. The present view is that orthogenesis is an unnecessary hypothesis; as a phenomenon it exists rather in the observer's mind than in the facts he observes. Yet the evidence indicates that something controls the pattern of evolution, and selection is capable of producing long-term trends in evolution, as well as extinction. Thus if an organism is favored with a structure which gives it advantages over its fellow-creatures, it may enjoy a higher survival rate until its offspring become a dominant part of the total population of its habitat. On the other hand, if it is genetically so maladjusted that it is incapable of living in the environment in which it finds itself, it will, of course, be exterminated.

But this is not all. Since all living creatures reproduce at rates far above those necessary to maintain their numbers were they all to live, it is evident that the survival rate must be correspondingly low, and this means the elimination of many individuals, often by purely fortuitous means. The best seed of a maple tree may fall upon a rock. The healthiest pup in a litter may be run over by a car. But there is further struggle and competition

among those not fortuitously destroyed, and here even minor favorable variations may produce a residual effect. Fitness to survive is relative — many individuals or groups may be good but others may be better. Should the environment fluctuate, then what was previously better may no longer be so, and supremacy may pass to a contemporary but previously less favored group. Thus there is a never-ending interplay between the variable organism and the variable environment, and, perhaps with the exception of man, it is the organism that must meet the demands of the environment, for rarely can the environment be controlled by the organism.

It is unlikely that the immediate environment is responsible for the initiation of the changes that adapt the organism to it, any more than the stencil directs the inkspots to fall within it. Few mutations examined under controlled conditions, that is, under conditions where they can be preserved long enough to be examined, are conducive to survival. And this is true of natural mutations as well as of those induced artificially. But for mutants that survive at all, environment often determines whether or not they will continue to do so.

Mutations and Changed Environment. Some few mutations would be advantageous under changed living conditions. The mutation for winglessness in the fruit fly *Drosophila* ordinarily produces abnormally high mortality. Under conditions of crowding and malnutrition, however, the mutant wingless fly survives as readily as the normal fly and perhaps even more so. Wingless butterflies on Kerguelen and other storm-swept islands of the far southern oceans survive there as successfully as winged forms in Africa or South America. Perhaps winged forms were blown to the islands, where, in the course of time, they gave rise to wingless mutants. Under ordinary conditions a wingless butterfly would probably be at considerable disadvantage, but special conditions on the islands seem to have given this mutation survival value. These islands are small, subject to strong prevailing winds, and surrounded

¹ For other aspects of variation, see Chapter 24.

by open ocean for hundreds of miles. Hence a large-winged, slow-flying butterfly might easily be blown to sea, whereas the wingless variety would not. If the wingless form was in other respects able to survive, the normal advantages and disadvantages would be reversed.

Environment as Selector. Similar reasoning is advanced to explain the prevalence of white animals in arctic regions. As far as is known, white mutants are as likely to arise in the jungle as in the Arctic. But selection favors white in a white environment, though not necessarily in others. Animals living in perpetually dark caverns are frequently not only white but also blind. Whiteness could persist there because color or its absence would be unimportant in a lightless world.

Blindness is more to be expected than whiteness in cave animals, though not for the most obvious reason. It is tempting to infer that a creature like the Mexican cave fish is blind because its ancestors did not need eyes and did not use them, so that they degenerated until eventually the offspring were born blind. But as we have seen, all the evidence is against this simple explanation. Rather, the blindness is probably the result of a number of mutations which might just as readily have occurred in a sunlit pond at the surface of the earth. Mutations for defective eyes are by no means rare. Eyes in a young fish are very large, and in some cases make up 25 per cent or more of its body weight. An eyeless cave fish, which does not waste one quarter of his substance on useless organs, would have an advantage over one with normal eyes. But even were there no advantage or disadvantage at all in eyelessness, such a type might well supplant the other by chance alone.

Similarly, white and other colors which offer little protection against the environment are common under conditions of domestication. Man produces an artificial, safe environment under which any color favored by him may thrive. He has even propagated such monstrosities as featherless pigeons, hairless mice, rhino mice, pirouetting mice, and endless albinos. Man himself has come in for his share

of mutations, most of which are anything but blessings. Of this kind are hemophilia, color-blindness, brachydactyly, lobster claw, astigmatism, glaucoma — to mention only a few.

Abundant as the evidence is that mutations occur at random and that the environment exercises a selective effect upon them, it must be admitted that this is not a complete explanation. Chance, too, particularly in small populations, may bring about the establishment of mutations as group characteristics, even though the mutations are not advantageous or are even rather harmful. At the present time, however, the ideas just outlined represent the best thinking of biologists on this subject. If the results produced by this apparently haphazard method appear to be too perfect to have been thus achieved, it may be pointed out that even in everyday life almost unbelievable results have come about through the operation of blind chance and coincidence.

Isolation

The function of the fourth factor in the evolutionary process, isolation, is perhaps not so obvious as that of the others. If variation, heredity, and selection operate together in a general community, we may expect increasing adaptation to the environment. We would not, however, expect a diversification of species, but rather, a slow replacement of one form by a better one. Yet if all organisms trace back to a common ancestor, there must have been a branching of the paths, not once, but many times. Any favorable mutation in a community would tend to spread through the entire community, thus changing it in its entirety in the course of time. For diversification, that is, for the creation of a new species, to occur, mutations appearing in one part of the community must somehow be prevented from spreading throughout the community. In other words, some form of isolation must operate. Many conditions can play such a role. Organisms may be washed onto the shores of distant islands and separated from the remainder of their species. Land areas once joined may be separated by geological events.

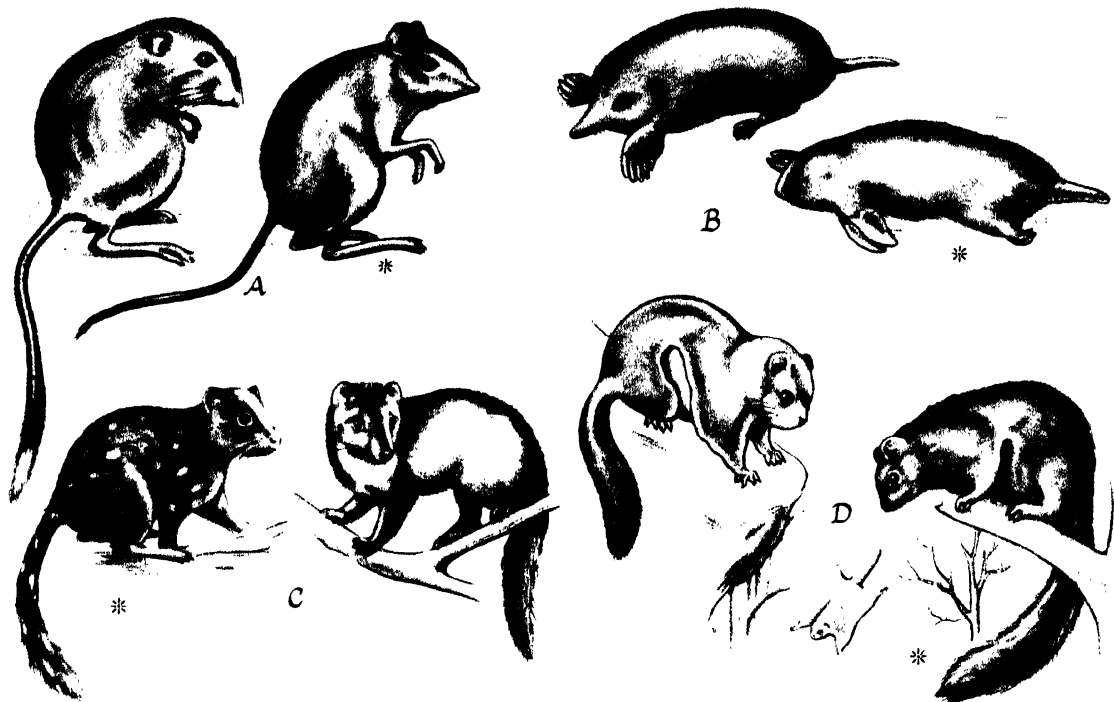


Fig. 108. Superficial similarity between pairs of marsupial (starred) and placental mammals is evidently a result of similar environment in which they evolved. A. Kangaroo rat (*Dipodomys spectabilis*), *rat-Kangaroo (*Betlongia*). B. Mole (*Scalopus latimanus*), *marsupial mole (*Notoryctes typhlops*). C. Marten (*Martes americana*), *native cat (*Dasyurus maculatus*). D. Flying squirrel (*Glaucomys volans*), *flying phalanger (*Petaurus sciureus*).

Animals may wander far afield, crossing but not recrossing barriers usually insurmountable, perhaps under the pressure of famine. Mutations may arise which cause a change in the breeding season or breeding locality, so that plants or animals living side by side are as effectively isolated from each other genetically as though they lived a thousand miles apart.

Geographical Isolation. The most obvious form of isolation is geographical, where two or more groups belonging to the same species are separated by a barrier such as a mountain range, a wide river, a stretch of open ocean, or mere distance. It is evident that under such circumstances a mutation in either group would be confined to that group, except for occasional migrants from one to the other. Since mutations are random, there is little chance that the two groups would change in precisely the same way, so that in the course of centuries the two might slowly diverge until they became

two distinct species. Once this has happened, effective isolation would be maintained because of the difficulty or impossibility of cross breeding (or breeding between different species) even were the geographical barriers to fall.

The effectiveness of geographical barriers in creating species frequently appears in nature. On the more than three thousand islands comprising the Philippine group, with a total area of only about 115,000 square miles, there are over 1000 species of land snails. On the almost 500,000 square miles of land in Siam and French Indo-China, there are only about 600 species of land snails. It is difficult not to see the reason for this difference. The continuity of the land area in the latter region offers far less chance for the formation of isolated groups than does the scattered land mass of the Philippine group.

Perhaps the most striking example of large-scale isolation in extent of space and time is

presented by Australia. The fauna of Australia has survived as a result of the isolation of that continent from the main land mass from the late Cretaceous on, so that the primitive mammals there evolved along independent paths. Early placental mammals, which had arisen somewhere in the Old World, had not yet dispersed to that region, and the marsupials and egg-laying mammals were spared their competition. Australia shows not only that isolation produces new species, but that environment can achieve similar adaptations even with an assortment of different and unrelated mutations. Thus Australia has achieved animals that are similar superficially to our squirrels, rats, chipmunks, minks, and kangaroo rats (Fig. 108), although they do not even belong to the same sub-class (see Appendix A).

The Breeding Unit. Less obvious but perhaps just as important as a means of isolation is the breeding unit. It is generally held that minor differentiations arise by small mutations, which are more likely to be viable than large or drastic ones, and that the cumulative effect of such small mutations eventually results in new species. One of the difficulties in understanding how a new mutation could spread throughout a species lies in the fact that, as far as is known, a new mutation is an isolated event and may not be evident in the offspring for a long time. Most species consist of millions of individuals, and thus a new mutation runs the grave danger of being scattered and submerged in the mass of individuals composing the species. The chance for a new mutation to assert itself would appear feeble indeed, were it not for the existence of small breeding units within the larger group. For a new mutation to become rapidly concentrated and thus effective within a group of organisms, the group must be limited in size. The new mutation can then emerge and be tested. Thus isolation of organisms within limited breeding units appears to be of the highest importance not only for the sake of the creation of new species, but for evolution generally.

Some such form of isolation is general. Species of birds, for example, are not, as they may

at first appear, single continuous populations with no isolating mechanisms between them. On the contrary, innumerable smaller breeding units are as a rule scattered over large areas, so that the species is more like a disjointed mosaic than an integrated unit. The chimney swift, for instance, will return to the same plot of ground, perhaps the same flue in which it was hatched, year after year. The same kind of units exist among migratory fish. The salmon, with all the coastal rivers open to it, will return to the river, the brook, and even the very rivulet in which it was spawned. In a world of apparently unlimited horizons, the mating horizon comprises only a few acres or a few square miles of land or water, and hence only a limited number of individuals. Within this invisibly bounded island, the organism will find its mate, and a mutation arising within the sphere will quickly travel to its limits. Beyond these, it is unlikely to penetrate. This is evident in the many local variations, races, and subspecies which abound wherever plants or animals are studied. There is, of course, certain to be overlapping at the edges of these breeding spheres, but the boundary is there even though it may not be sharply defined. Actual geographic continuity by no means indicates continuity of germ plasm, even within a given species. Thus while two related species of toads, *Bufo americanus* and *Bufo fowleri*, live in practically the same area, can easily be crossed, and have apparently fertile offspring, they do not generally hybridize in nature. In this case, the isolating mechanism is not clear.

Other Types of Isolation. This type of isolation, created by the habits of the creatures, is perhaps one of the least apparent, though most potent, forms. More obvious kinds of isolation appear on every hand. Mutations arising within a slightly isolated group frequently tend to increase the isolation by creating new barriers. Plants within a group may be so changed as to have an earlier or a later period of blossoming. Obviously a blossom that has already been pollinated can no longer cross with a plant that blooms later, although the two may belong to the same species and

thus may be perfectly capable of cross fertilization. Mammals in one area may so change in color or appearance as to become unattractive or repugnant to others in a neighboring sphere, thus effectively isolating the two groups. It has even been related that chimpanzees with a pinkish skin show reluctance to mate with those that have a dark skin.

Differences in physiology, although not apparent to the eye, may also serve as isolating barriers. If any two groups of organisms within a species are so constituted physiologically that their offspring are not so likely to survive, or are less fertile than the norm, an effective barrier between such groups is established. Moreover, this barrier will tend to produce even greater differences, and eventually may separate the groups entirely. Thus horses and donkeys, though closely enough related to mate, are sufficiently different in their genetic structure that their offspring, mules, are generally sterile. The germ plasm of horses and donkeys is effectively isolated.

Mere difference in physical structure may serve to isolate otherwise miscible groups. Ordinarily, the crossing of a Newfoundland dog with a Pekinese is unlikely, though perhaps possible. Similarly, a Bantam cock appears unable to mate with a hen of ordinary size.

Isolation is of many kinds, and mutations arising within one isolated group increase the effectiveness of its isolation. Darwin's explanation of the origin of new species, that they evolved from divergent races of a common species through a gradual accumulation of small genetic changes, still appears to be the best yet offered and is probably correct, although a minority of biologists oppose it.¹

SOME PROBLEMS IN EVOLUTION

The whole problem of understanding the mechanism of evolution is complicated by the fact that it is often hard to tell whether a given trait is inherited or acquired, and frequently

¹ For the Darwinian view, see especially Dobzhansky, *Genetics and the Origin of Species*. For an expression of the opposite view, see Goldschmidt, *The Material Basis of Evolution*.



Fig. 109. The "dead leaf butterfly," *Kallima*. Note the perfection of design, even to the "midrib" of the leaf.

only the most careful examination and experimentation will show. A few examples will illustrate the difficulty. For convenience we may classify such traits as (1) characteristics that are definitely inherited but appear to be acquired; and (2) characteristics that appear to be inherited but are probably acquired.

Deceptive Inherited Characteristics

Clearly of this type are protective coloration and mimicry in animals and plants and special forms of behavior in certain animals.

Protective Coloration and Mimicry. Many organisms are so colored as to blend more or less into their natural background and thus to escape detection and molestation. The brown-gray peppered coat of the defenseless rabbit makes the animal as inconspicuous as any coat it could have. Certain leaf-hoppers and butterflies can hardly be distinguished from the leaves around them (Fig. 109). Shrimps imitate the color of the plants on which they live. Some butterflies that are inedible for birds appear to be imitated in color and design by others that are perfectly edible — though in this case other factors besides protective coloration may be involved (Fig. 110).

Moreover, this imitation goes well beyond color and by imperceptible degrees moves into the behavior patterns and even the form of an organism. An insect called the walking stick looks amazingly like a dried twig. Harmless

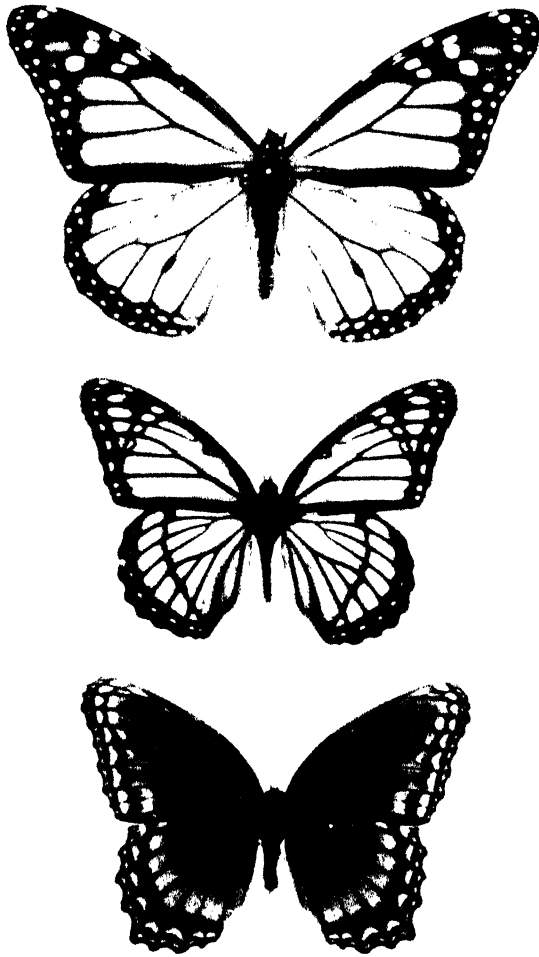


Fig. 110. The edible Viceroy butterfly (*Basilarchia archippus*), middle, imitates the nauseous Monarch butterfly (*Danaus plexippus*), above. Below, a related variety.

snakes imitate poisonous ones in behavior as well as color. Certain flies and butterflies mimic bees and wasps with great fidelity. The caterpillar of the spicebush butterfly produces a distinct shock on a thinking human being, and may be no less shocking to a foraging bird. Rolled up in a protecting leaf, only the "head" of the little monster protrudes, which looks most convincingly like the head of a snake with staring, glistening eyes. The effect is heightened by the protrusion of a forked orange "tongue," just where a snake's tongue ought to protrude, when the cater-

pillar is irritated. Color spots which resemble eyes are sculptured on the bulging back of the animal, which looks like a head, so that they stand out, while glistening pigment actually makes them shine as though moist. The actual head of the insect is a tiny knob at the front and bottom margin of the sham head.

Certain insects have taken up their abode in ant colonies. Some of them have succeeded in becoming welcome guests by secreting substances relished by the ants, while others masquerade as ants and thus escape eviction. Among guests of seeing ants an astounding similarity is achieved by color patches and markings, so that bodies of a thick waisted form take on the slim-waisted appearance of their hosts. Among blind ants and sightless termites, the guests may differ entirely in color and design, but their bodies are so constructed in form that they must feel like ants — or termites — to the questing antennae of their unwitting hosts.

Clearly such adaptations by mimicry and adaptive coloration are products of evolution, and their function is in most cases obvious. But the way in which this imitation is achieved is less easily understood. No mechanism is known whereby close association would make an insect look like a leaf, and certainly none whereby one butterfly would come to look like another with which it never comes in contact. Difficult as it is to imagine how some of the highly perfected imitations could have been achieved by chance mutations, there is no better explanation at hand. Any mutation that would cause a pursued and edible butterfly to look even remotely like an inedible one might increase its chances of survival individually and as a species. Only the prolonged selection of a succession of such fortuitous mutations could produce the striking results so often found in nature.

Special Forms of Behavior. Another type of inherited characteristic which may appear to be acquired is illustrated by the behavior of some young European jackdaws. These are sleek black birds about the size of pigeons, with a pearl gray collar around the back of the neck.

Wishing to study these interesting birds, we raised a group of nestlings in a large cage. They were fed small sausages of soft prepared food which we pushed far into their eager, open mouths. They soon learned the procedure and expressed hunger by opening their beaks and giving a loud and peculiar hunger cry. Water was served them several times daily from a glass which was held before them. In drinking, they would insert their beaks, as most birds do, then raise their heads and swallow. Bear these facts in mind in visualizing what now happened.

One morning an almost fully grown jackdaw stood on a table, and a beetle was placed in front of it. Although the bird had never seen a beetle, it at once opened its beak in its habitual I-want-to-be-fed manner and gave its characteristic hunger cry. This brought no result, so it pecked at the beetle and quickly ate it. At about the same time, when water was presented as on all previous days, the young jackdaw suddenly began an unusual maneuver. With its beak in the water, as though to drink, it squatted low on its perch, flapped its wings in short jerky beats, and waggled its tail from side to side. Suddenly it became clear that the bird was taking its first bath — and though only the tip of its beak touched the water, it went through the complete bathing ceremony of throwing water over its back with its wings. Of course it remained perfectly dry during the whole procedure. It had never witnessed another bird bath, nor had it ever had an opportunity to bathe itself.

The implications of this observation are quite clear. A bathing bird efficiently wets every part of its body, splashing water over its back, rubbing its head from side to side, and wagging its tail. Ordinarily the process looks as if it were deliberate and probably learned. The feat of recognizing a beetle as an edible article would also appear to be a learned characteristic. However, the conditions under which these birds had been raised make it necessary to assume that the entire pattern of behavior was inborn. The Lamarckist would say that the actions of its ancestors

had been passed down as inherited qualities to the offspring. The biologist today would look for the answer in a pattern of adaptive behavior selected from an almost unlimited number of possible patterns produced by fortuitous mutations.

Deceptive Acquired Characteristics

While it is often difficult to be sure of characteristics which are definitely inherited but seem to be acquired, it is sometimes equally difficult to classify traits which appear to be inherited but are probably individually acquired. Of this kind are the migrations of fish and of birds, and perhaps the habits of cats in catching rats. The migration of fish and birds was long regarded as an outstanding example of the mysterious nature of instinct, that is, of inherited patterns of action. Although we are not yet certain of all the factors involved in producing the phenomenon whereby a fish will return to the stream of its birth, or a bird to its nesting site after a flight of thousands of miles, the pattern is beginning to lose some of its mystery.

It now appears that a fish has an astonishing capacity for remembering the path it traveled when newly hatched, and thus returns to the same spot when it in turn is ready to spawn. Its progeny will, of course, in their turn seek the same river, for that will be the place where they were born. Evidence for this is the fact that it has been possible to train whole races of migrating fish to use new streams when their old ones were cut off by waterpower dams. Such retraining can be achieved by merely transferring eggs or newly hatched fish to a new stream.

Similarly, it does not appear that most migratory birds possess mysterious knowledge whereby the young birds make their vast trips, for the young usually fly with the oldsters who have made the trip before. In the following year they will be the oldsters, and will serve as guides for the next generation. Thus the same families and groups return to the same breeding places year after year and generation after generation, unless some accident or slip

in memory leads them astray. Yet in both cases the instinct to migrate, as distinct from the choice of route of migration, is probably inherited.

Similarly, it has been shown experimentally that cats do not "instinctively" catch rats, but must learn to do so. Certain patterns of behavior, then, are clearly acquired, though superficially they may look as if they were inherited. The fact that it is often hard to be sure whether a given trait is inherited or acquired adds considerably to the biologist's problems.

EVOLUTION: AN EVALUATION

Our analysis of evolution and the forces behind it has yielded at least a partial explanation of what has happened and how it has happened. But there has been no attempt to explain why it has happened. If we hope to find an answer to this question — and as biologists we need not, though as human beings we may very well wish to — we must try first to evaluate the results of evolution, and we must do so as objectively as possible. We cannot, for instance, evaluate all other creatures merely in terms of human faculties and achievements, such as intelligence and speech. Rather, we must attempt to see man along with all other living creatures in terms of some general rather than some merely human standard.

The only clear standard which is immediately visible is success in the struggle for survival. No other attainment, however lofty by human notions, appears to be of any significance in long-range terms if the species fails to survive. This fact is so self-evident that it may appear unnecessary to stress it, but because of its very obviousness it was frequently overlooked until Darwin called attention to its real significance.

Beyond this we may recognize another standard, control over and independence of the environment. On this criterion it may be said that the amoeba is "higher" than the simple organic molecule, the honeybee higher than the earthworm, man higher than the ape. For clearly each is less at the mercy

of its environment than its predecessor is; each has a greater degree of control over the circumstances in which it lives.

Complexity, Progress, and Regression

Beyond this, is there any one standard by which organisms insure their ultimate survival? There seems to be none. One of the most striking results of evolution has been a steady increase in the complexity of organisms. In fact, evolution has been defined in terms of the increasing complexity of life. But complexity can hardly be considered valuable for its own sake. Rather, it should be looked upon as a means to increased efficiency, which in turn enhances the organism's chance of survival. Yet it is abundantly evident that complexity is not necessary for survival, or not, at least, for immediate survival. Bacteria, which are among the simplest, most primitive, and probably oldest living forms, still exist, and will probably continue to do so indefinitely. Complexity in itself, then, can scarcely be considered an end-result but merely another way of achieving survival.

Along with complexity there appear two opposite trends in the process of evolution: a steady and apparently inexorable "upward" pressure of the great mass of life, and at the same time frequent regression and disappearance of individuals and whole groups. Life came slowly out of its cradle of water, rose above the muddy shore, spread over the surface of the earth, and even soared into the clouds. On the other hand, representatives of these triumphs of evolution, such as the whale, the porpoise, and the dugong, have lost their adaptation to land life and reverted to the fishlike pattern from which their ancestors had evolved millions of years earlier. The penguin and the ostrich have lost their wings as flying instruments. The crustacean parasite *Sacculina* abandons its eyes, its complex nervous system, its digestive tract, and its intricate locomotory organs in order to become an inert mass of reproductive tissue. Countless other species, of which the mastodon and the giant reptiles are only the most obvious examples,

have been exterminated even though they once seemed to dominate the earth.

In the process of evolution species relentlessly competes with species, and individual with individual. Each lives and rises above the waters of oblivion by standing upon the struggling forms of the creatures beneath. Life appears to be the cheapest and the most abundant of commodities and is spent with a profligate hand. Thus it can scarcely be said that evolution is all progress; rather it implies only survival, based on the ability to compete in a heavily competitive world.

Out of this struggle emerges the nicest adjustment between creature and environment. The evolution of an organism at any given moment is limited above as well as below. The speed of the predatory animal must clearly be up to a minimum standard determined by the speed of the animal upon which it preys. If the predator is too slow it must needs starve. But it may also starve if it is too fast, for then it may simply exterminate its prey, and thus cause its own extinction in turn. Organisms are evidently molded to the strict and narrow specifications of their environment. The stencil is sharply cut. And still the only evident end is survival.

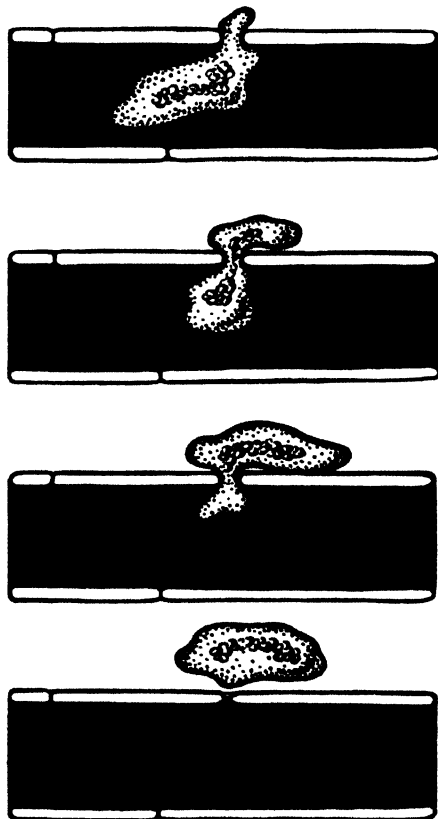
Yet despite the regression, degeneration, and elimination of individuals and entire groups, the over-all picture of evolution suggests an upward trend. No creatures of the past equaled birds in perfection of adaptation to flight, or mammals in brain development. The increase in complexity sometimes brings with it, in certain dominant lines, *an increase in adaptability to and mastery over the environment*. The best of today is clearly better than the best of the past; and this may be considered progress within the mass of life by any standard of measurement.

The course of evolution may be compared to a maze of branching and rebranching paths, most of which come to a dead end. Some of these paths extend much farther than others, while some few, perhaps, lead on indefinitely into the future. Picture a number of animals released into such a maze. They will have to

proceed blindly, for they cannot see where their paths will lead them, and so most of them will eventually end in some blind alley, that is, in extinction. The faster an organism proceeds along its path, the sooner it is likely to find itself at the end of its road. The more it loiters along the way, the longer its ultimate fate still rests in the future. A lucky one here or there will have traveled far along a promising path, though the danger of going into a *cul de sac* still confronts it at every turn. Because they have made the most turnings, the organisms that have gone the farthest are the ones most likely to have chosen a wrong turn already. The loiterers still have their "mistakes" to make.

Because a high degree of specialization usually reduces adaptability to changed environment, the most highly evolved organisms of

Fig. 111. White blood cells lead an independent life within our bodies. Leucocyte passing through a capillary wall.



any one era tend to stem from the less highly specialized and more adaptable types of the preceding era rather than from those most advanced. Thus all present species are either momentarily or still successful types or are loiterers that did not join the race and thus avoided the wrong turnings. These latter are not yet entirely eliminated from the contest, but it becomes clear that ultimate survival in the face of keener competition by more advanced and efficient creatures will not be possible for creatures that do not change. Change is an essential part of evolution. The organism that avoids change may avoid errors today, but it is likely to miss the path that leads to ultimate survival (but see Fig. 111).

Rapid progress along lines of narrowing specialization is likely to lead to early extinction. Long-term progress toward wider, generally increased efficiency is beset on either hand by

the danger of turning off into some side-branch of narrow specialization.

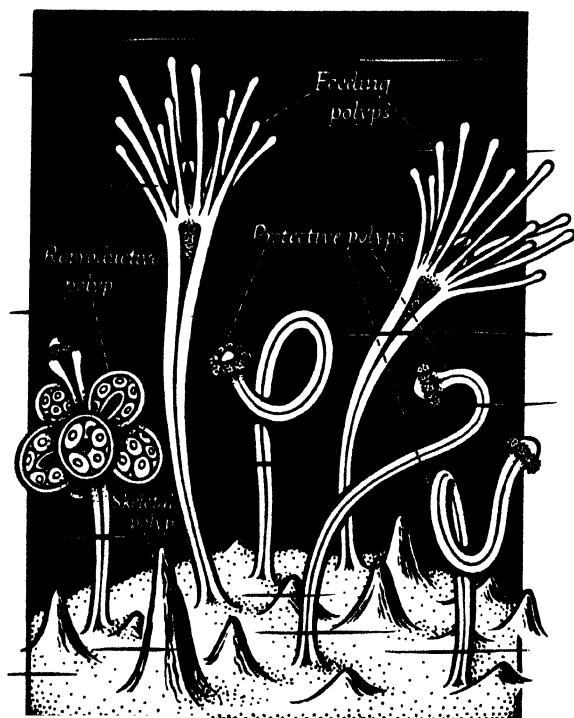
Evolution in Levels of Integration

Yet in the long view evolution does seem to be a thing of successive levels, so that the "highest" developments of succeeding ages appear to have added something to the total. It is easy to trace the main levels, from inorganic to organic, from single-celled to many-celled; from individuality to collectivism. Perhaps the most interesting of these levels is the one last named. Man represents a high degree of specialization in one line and one alone. He has not concentrated on any narrowly limited ability, such as swimming, climbing, or flying. Man's chief specialization, rather than limiting his adaptability, has enhanced it. The instrument of this broadening specialization is, of course, his brain. But beyond this unique mental development, he has followed a pattern of evolution that has proved its effectiveness many times in the past: he has evolved toward collectivism. His evolution in this direction is still young; nevertheless, the marvels of civilization and of modern technology are the product of man, the social organism, not of man the individual.

Collectivity came into play when single-celled animals became colonial organisms; when colonies become multicellular; when many-celled creatures banded together to form states and "super-organisms" as in certain coelenterates, social insects, and man. Many organisms exhibit a tendency to seek higher levels of integration, even before a lower level is fully realized.

Simple "Collective" Organisms. We may briefly view this peculiar phase of evolution in the colonial coelenterates and in the slime molds, or Myxomycetes, in order to see it in its elementary state. In their individual structure, coelenterates are among the simplest multicellular organisms. Yet some of them have evolved a highly specialized colonial organization. In *Hydractinia*, which forms colonies on the shells of hermit crabs, the individuals, called hydroid polyps, have differen-

Fig. 112. Polymorph coelenterate colony (*Hydractinia*). Differentiated polyps are mutually interdependent. The individuals have attained only a relatively low degree of integration, but the integration of the social unit is relatively high.



tiated into three distinct types: feeding polyps, reproducing polyps, and stinging protective polyps (Fig. 112). None of these types can get along without the aid of the others. While individually they are small and insignificant, collectively they are formidable creatures, such that one related variety, the Portuguese man-of-war, is feared even by man.

In the slime molds, organization at a new level is achieved within a single individual. These creatures, which show plant as well as animal relationships, reveal an amazing life history. The organism hatches from a single immobile cell (a spore) as a tiny whip-bearing cell called a flagellate. Under conditions favorable to individual survival, such a swimming cell will withdraw its locomotory whip, or flagellum, and will metamorphose into a formless cell that moves by protruding parts of its cytoplasm somewhat in the manner of the protozoan amoeba. The little myxomycete then reproduces by cell division until hundreds or thousands of cells, many produced from other cells, will swarm about on a common food material, or substrate. If unfavorable conditions arise, these cells tend to aggregate in groups which finally fuse completely, forming a large mass of protoplasm containing many nuclei. One end of this mass may then become a dominating head-end, and will lead the movement of the entire mass, which eventually forms a common fruiting body and once more produces spores (Fig. 113). Thus, in the slime-mold, the individual yields its independence to become a subordinate part of a super-organism in a certain phase of the life cycle.

Collectivity in Man. The similarity between the biological behavior of this creature and the social behavior of man is not difficult to see. Its differentiation both as an individual cell and as a cell community is low, but its integration far surpasses the social integration achieved by man. In past evolution, the biological integration of individuals into super-organisms has been achieved by an inborn compulsion on the part of each individual, not by coercion. Man alone has dared the task of social organization on the basis of

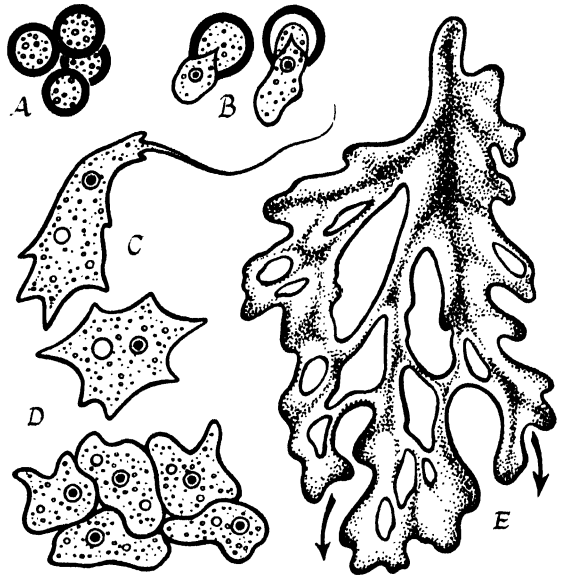


Fig. 113. Mobile phases in life of slime mold. *A.* Spores. *B.* Spores germinating. *C.* Amoeboid zoospores, one flagellated. *D.* Zoospores associating to form a plasmodium. *E.* Plasmodium flowing in the direction indicated by arrow.

voluntary, learned behavior. Whatever else these examples may teach, they do illustrate the tendency of many organisms to evolve integration at successively higher levels. The increasing control over his environment which man may attain through this kind of evolution suggests its value in promoting long-term progress.

Is There an Ultimate Answer?

These considerations bring no answer to the persistent question why all this goes on; nor is it considered the business of science to seek such an answer, though as individuals we may wish to do so. Our attempts to find an answer are always rewarded with the conclusion that this or that process increases or decreases the probability of survival, and that is as far as we can go. Perhaps there is no further answer. But perhaps, also, the fact that we can find none stems from our own mental limitations. A mind forever living within the motor of a car might conclude that the piston moves in order to expel the burned gases left in the cylinder after the previous firing stroke. This is, of course, not altogether wrong, but it is

limited. For it fails to consider that the movement also transmits power through the crankshaft to the wheels and thus drives the car to some human destination. It is conceivable that the mind of man in similar fashion sees only a fragment of a larger pattern whose purpose he can scarcely guess.

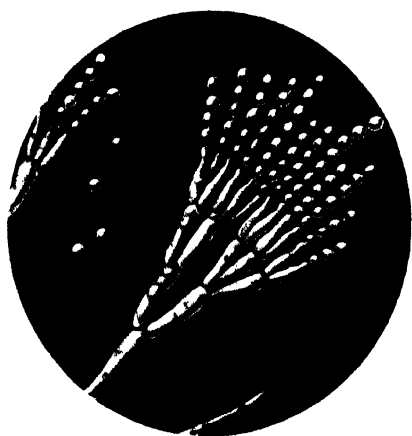
True, man today can see far more than any creature before him. His mind enables him to peer at least a little way over the walls of the evolutionary maze. He can look back over the path along which he has come, and he can see, though dimly, where some of the paths ahead may lead. Thus he can begin to choose the path which may avoid a possible dead end. He should begin to see, among other things, that the principle of increasing integration should not be violated — that war must be renounced, co-operation vastly increased, and the earth's resources more fairly distributed. Man can see these things and many more, and he is the first creature on earth to have evolved this faculty. History will tell whether he had the wisdom to use that vision.

Despite the fact that man can see so much, he is far from anything that yet looks like an answer to the ultimate why. The fragmentary facts of evolution, as revealed to the human intellect, seem to show no purpose beyond the

struggle to survive. Yet it is scarcely wise to assume that the limited mind of man, with its limited knowledge, has necessarily been able to grasp the ultimate nature of things. As we scrutinize the threads in the tapestry of life, perhaps all we can hope is to discover some of the rules by which color and design are incorporated into it. If we fail by this method to see a pattern in the whole, perhaps we are merely nearsighted. It would be foolish indeed to say that because we find no pattern there can be none; it would be equally foolish to assert categorically that there is one. Even our brief survey of evolution in these last three chapters has given evidence that progress has taken place. If, as some insist, this implies mentality, consciousness, and intent in the nature of the universe, we must admit the possibility of such intelligent guidance. But we cannot prove its existence any more than we can deny it. If a mechanistic approach to these problems appears to be incompatible with such a statement, that is perhaps because we all too easily overestimate the intellectual powers of man. Finally, if purpose implies intelligence, it may be significant that the apparently purposeless process of evolution has at least produced in man a creature capable of the concept of purpose.

PART FOUR

THE WORLD OF PLANTS





Among plants and animals alike, odd quirks of fate may spell survival or extinction. Above is a branch of the maidenhair tree, Ginkgo biloba, which exists today only because it was for centuries cultivated in Chinese temple gardens.

Primitive Plants: Bacteria, Algae, and Fungi

The dynamic phenomenon of life has been shown as part of a continuous evolutionary process that probably began with the beginning of the universe, though life itself is a comparatively recent development. The viruses are borderline structures between the animate and the inanimate, though there is still a vast gap between the most complex inorganic molecules and even the simplest of these organisms. Nevertheless, these substances — or creatures — more nearly bridge the gap between living and non-living things than anything else now known. We have seen that some, if not all, of the activities of protoplasm may be interpreted in terms of physics and chemistry, and have thus removed part of the mystery. Finally we have seen something of the mechanism by which the process of evolution operates. Yet all this is only the general picture, and there is a great deal still to be filled in. First we shall look more closely at the world of plants.

Classification

The plant kingdom is divided or classified into five main groups called *phyla*, ranging from the simplest of organisms which can definitely be called alive to the most highly evolved of trees and flowering plants. The animal kingdom is similarly divided into *phyla*. Each phylum, in turn, is subdivided into successively smaller categories down to the smallest distinguishable biological group. Two examples of the scheme of this subdivision appear on the following page.

We shall not go into further details of classification here, since the major outlines of the scheme for both plant and animal kingdoms are given in Appendix A. The listings there presented will well repay any efforts made to

consult them frequently, for properly viewed, they can serve as a guide to the dynamic and evolutionary nature of the development which will be traced in subsequent pages. In this chapter we shall consider the two plant phyla which stand lowest on the evolutionary tree.

SCHIZOPHYTA BACTERIA AND BLUE-GREEN ALGAE

The first of the great plant groups is the phylum *Schizophyta* (Gr. *schizein* = to split + *phylon* = plant), so called because schizophytes reproduce by division or splitting. These are the simplest of all plants — indeed in many cases they are not clearly plants at all but might almost as well be considered animals; or, more accurately, they have not in all cases become sufficiently specialized to belong definitely to either group. They are also the simplest organisms that can certainly be called alive. The schizophytes are clearly organic, but they have apparently not developed to the point where they have mitotic cell division, and some of them even lack typical cell nuclei, and so are not even cells in the usual sense. This phylum contains two large subgroups or classes, the bacteria and the blue-green algae.

The Bacteria

Forms and Types. As a group, the bacteria are the smallest and least highly developed of all living things with the exception of the controversial viruses. There are hundreds of different types of bacteria, ranging in size from 0.2 to 25.0 or more μ (microns), that is, thousandths of a millimeter; and while they are large in comparison with atoms and molecules, they are minute compared to most other living things. Not only are the bacteria amazingly

Kingdom	<i>Animalia</i> (Animals)	<i>Plantae</i> (Plants)
Phylum	<i>Chordata</i> (With a notochord)	<i>Spermatophyta</i> (Seed plants)
Subphylum	<i>Vertebrata</i> (With a backbone)	_____
Class	<i>Mammalia</i> (Mammals)	<i>Angiospermae</i> (Flowering plants)
Subclass	<i>Eutheria</i> (Placental mammals)	<i>Dicotyledoneae</i> (With two cotyledons)
Order	<i>Carnivora</i> (Flesh eating)	<i>Sapindales</i> (The maple order, named after soapberry)
Family	<i>Canidae</i> (Dog-like)	<i>Aceraceae</i> (Maples and related)
Genus	<i>Canis</i> (Dog)	<i>Acer</i> (Maple)
Species	<i>Familiaris</i> (Domestic)	<i>Saccharum</i> (Sugar)
Subspecies	Sheepdog	_____
Race	Scotch collie	Local variety

varied in size, but they also cover a considerable range in shape and form (Fig. 114). Some of them, called bacilli (L. "little stick") are shaped like rods and are of varying lengths. Others, called *cocci* (Gr. "grain-like") are spherical. Still others, the *spirilla* (Gr. "coil"), take various corkscrew shapes. While the individual bacterium is a single unit of protoplasm which may be called a bacterial cell, in many varieties these units do not become separated from each other as do many single-celled organisms, such as the protozoan amoeba for instance. There are several sorts of colonial groupings among bacteria. Some grow in pairs and are called *diplococci*, like the organisms which cause pneumonia and gonorrhea. Some form long chains like strings of minute beads, as do the sore throat *streptococci*. Others form cubes (the *micrococci*), clusters (the *staphylococci*), or slender filaments similar to molds (the *microbacteria*), and these filaments may even show considerable branching. In this tendency to form colonies of various shapes and kinds, it may be said that the bacteria foreshadow a tendency which becomes marked in the next two higher plant groups, the algae and the fungi.

Many bacteria are capable of movement, and while some have no apparent means of locomotion, others, especially among the rod- and spiral-shaped forms, are equipped with long, whip-like processes called *flagella*. These may be single, they may be in one or two small brush-like tufts, or they may cover the entire organism. The beating motion of these fine hair-like processes is capable of propelling the organism through the liquid medium in which it lives.

While the internal organization of the bacteria is primitive, and there is not an absolutely definite differentiation into cytoplasm, fully-developed nucleus, and cell wall, there are rudimentary evidences of all these structures. Nuclear structures are now known to be present in all bacteria which have been examined by suitable cytological techniques. The bacterium is surrounded by a thin, membranous covering, the outer part of which tends to break down

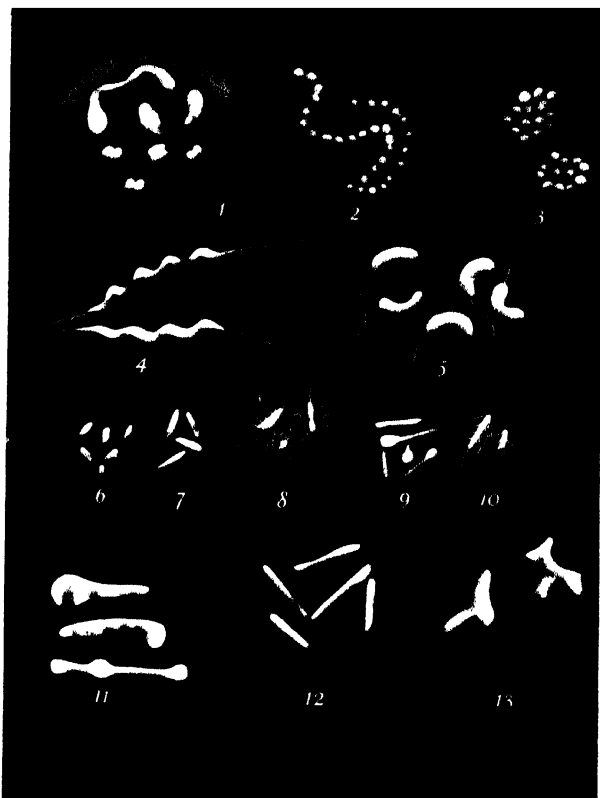


Fig. 114. Types of bacteria. 1. Gonococci in a blood cell (diplococcus). 2. *Streptococcus pyogenes* found in pus. 3. *Micrococcus aureus*, found in boils. 4. *Treponema pallidum*, cause of syphilis. 5. *Vibrio cholerae asiaticae*, cause of cholera. 6. *Nitrobacter*, soil bacterium transforming nitrites into nitrates. 7. *Thiobacillus thioparus*, a sulfur bacterium. 8. *Salmonella typhosa* (*Bacterium typhosum*), cause of typhoid. 9. *Clostridium tetani*, cause of lockjaw. 10. *Clostridium tetani*, treated to show flagella. 11. *Corynebacterium diphtheriae*, various types, cause of diphtheria. 12. *Mycobacterium tuberculosis*. 13. Involute forms of nitrogen fixing bacteria in root-nodule of bean. Sizes not relative.

into a kind of gelatinous coat or capsule around the organism. In some varieties, this is merely an outer covering. In others, it holds large numbers of individual units together in clumps.

Bacteria reproduce simply by fission. The cocci or spheres elongate, constrict in the mid-region, and divide. The bacilli and spirochetes divide across the middle. After fission, the new units may remain joined, the spheres in long chains or other groupings, and the rods in filament-like structures. Under conditions of optimum temperature and satisfactory food



Fig. 115. *Azotobacter*, nitrogen-fixing bacterium found in soil and sewage.

supply, bacteria reproduce at an astonishing rate, and divisions as rapid as one every fifteen minutes have been recorded, though the average rate is less rapid than this. Ordinarily, such conditions as changes in temperature, inadequate food supply, and other effects of the environment keep the rate down, yet their rapid multiplication is one of the reasons why the disease-producing bacteria are often so dangerous and so difficult to combat. Generally considered to be plants because of their apparent affiliation with some forms of fungi, especially in their branching growth and their reproduction by spores, many bacteria might nevertheless be equally well thought of as belonging to a separate group entirely.

Discovery and Importance. The first authentic description of bacteria is that of Leeuwenhoek, in 1683, though the idea that contagious diseases are spread by minute animals was expressed some years earlier by Athenasius Kirchner. Leeuwenhoek not only described bacteria but pictured their shapes and movements in drawings that were surprisingly accurate in view of the comparative crudeness of the microscopes he worked with. Knowing, as we do today, the astonishing reproductive powers of these microorganisms, and their as-

tonishing ability to resist conditions that kill all other forms of life, such as boiling for as long as sixteen hours, it is not surprising that early investigators believed that they arose spontaneously from inert matter. Such a belief is even less surprising when we recall that the theory of spontaneous generation had been generally and widely accepted, and that maggots, insects, and even birds and tiny human beings — homunculi — were thought to arise spontaneously in fermenting matter.

By a series of experiments, however, it was shown conclusively that microorganisms would not appear in media usually known to harbor them unless they were first introduced into it. Among the men who devoted themselves to this problem were Spallanzani, Schulze, Schwann, and Schroeder, but it remained for Louis Pasteur in 1862 to show conclusively that microorganisms appeared in suitable culture media only if they had access to it. The work of Pasteur conclusively disproved the theory of spontaneous generation. Beyond this, it laid the foundations for the modern concept of aseptic surgery and the principle of immunization and ultimately made possible the canning and food-processing industry.

Pasteur's investigations soon led him into the field of animal diseases, first to the study of pebrine in silkworms and then to the problems of anthrax and chicken cholera. Edward Jenner in 1796 had shown the practicability of immunization by introducing vaccination against the scourge of smallpox. But the world was not quite ready for a wider acceptance of the principle of immunization, and it fell to the personality and perseverance of Pasteur to place the principle on a scientific basis. After him, progress was rapid. Lister in England applied the knowledge of germs to practical surgery with striking results. Koch in Germany made spectacular advances in the culturing of bacteria, first on gelatine and then on agar-agar, a seaweed preparation, and knowledge thus gained led to further immunization practices. In the year of his death, 1906, Ehrlich, famous for his "606" or salvarsan, made the first successful attack on one of the prime

bacterial killers, the dread syphilis spirochete.

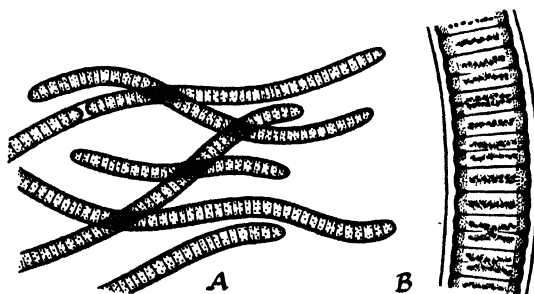
Though the story of man's defensive methods against bacterial diseases is spectacular, it must not be thought that all bacteria are inimical to man's welfare. Indeed, while some are harmful, many are indifferent in their effect on man, and some are essential. In their role as converters of organic matter back into inorganic form, and in the ability of some to bind atmospheric nitrogen chemically so as to make it available to plants, bacteria are an essential link in the vital nitrogen and carbon cycles of nature (page 73-76). Finally, of practical use but hardly essential are the bacterial processes involved in industry. Among these are the making of silage from green crops for the feeding of cattle, the making of vinegar, the retting of flax and hemp, cheese-making, and sewage disposal. In all these processes, bacterial action results in chemical changes desired by man.

✧ *Nutritive Processes.* Bacterial nutritive processes run from almost animal-like to almost plant-like, though few bacteria have evolved the ability to tap the almost unlimited supply of energy from the sun. Thus bacteria are not capable of photosynthesis, as green plants are. Many of them, however, are capable of chemosynthesis; that is they put together the substances they need by means of chemical energy rather than energy of sunlight. Bacteria may be grouped as autotrophic and heterotrophic. The autotrophic ones are those which are independent of other organisms as a source of nutritive substances because they are capable of chemosynthesis. (Among these are the sulfur and iron bacteria, which oxidize these elements and with the energy thus obtained extract the carbon they need from the carbon dioxide of the air, as do green plants.) Their role in making sulfur and iron available for other living organisms is similar to that of the nitrogen bacteria in the nitrogen cycle. Also autotrophic are some of the nitrifying bacteria which transform ammonia and other substances into usable form, in the process making nitrogen available as plant food (page 74).

In contrast to the autotrophic bacteria, the heterotrophs are not able to synthesize their

own organic compounds but must draw some needed substances from organic sources. Some limit their demands to sugar (carbohydrate), as for example the nitrogen-fixing bacteria, which yield some of the nitrogenous compounds which they manufacture by chemically binding atmospheric nitrogen, in exchange for sugar manufactured by the green plants on whose roots they live. Also dependent on sugar produced by other organisms are the denitrifying bacteria which, however, render a disservice in return by freeing the nitrogen in existing nitrogenous compounds. Other heterotrophic bacteria require proteins as well as carbohydrates. Some of these are saprophytes (page 73), deriving the substances they need from non-living organic matter. Bacteria of this type have been found extremely useful in sewage disposal. Other saprophytes are parasitic, and get their food from living organisms. These are the disease producers, and their effects may take the form of toxins or poisons, interference with physiological function, or actual destruction of the tissues of the host. Still another group, as we have seen, produces fermentation. Thus the nutritive processes of some bacteria are extremely important to man and to the very existence of life itself, while other bacteria are among our most virulent enemies. Perhaps fortunately, however, the effects of many are neutral. While some bacteria are much like plants in their metabolism and others are much more like animals, their minute size, their great variety, and the difficulty of accurately determining the details of their metabolism often make it extremely difficult to tell just where they do belong in the world of living things.

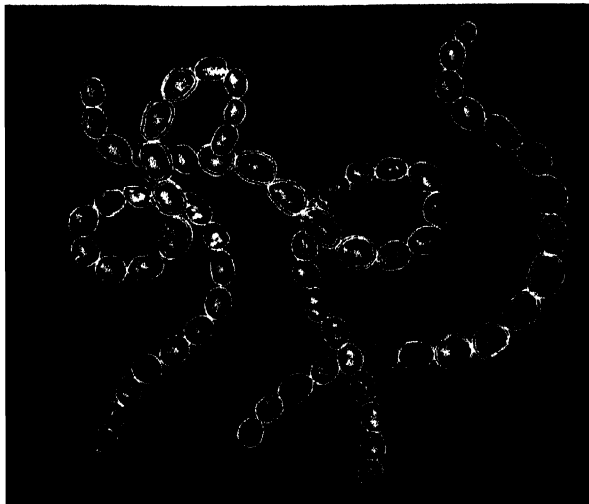
Fig. 116. *Oscillatoria*, a blue-green alga. Filaments and section.



The Blue-Green Algae

The second large group of schizophytes, the Cyanophyceae (Gr. *kyanos* = dark blue substance) or blue-green algae, show certain similarities in structure and behavior to the bacteria, such as in nuclear structures and reproduction by simple fission. These probably represent an ancient group that has persisted with most of its primitive characteristics unchanged. Found in fresh water, they may form dark, blue-black coatings on rocks, and some have colors that run into red and violet. They differ from other colored plants in that their coloring matter is not confined to chloroplasts but is distributed in the protoplasm. Common forms like *Oscillatoria* may be found in fresh water ponds (Fig. 116). The cells form long filaments, and perform peculiar undulating or weaving motions visible under the microscope. Hence their name. *Nostoc*, another member of this class, also assumes the form of a long slender filament, in appearance much like a bead necklace. However, its threads come coiled in little spherical balls of mucilage, so that, floating at the surface of a pond, they look exactly like fresh green peas. It is interesting that some members of this large group are found in hot springs, where they alone can exist, while others manage to survive in frozen antarctic lakes. Even in its simplest forms life is remarkably stubborn and persistent.

Fig. 117. *Anabaena*, minute fresh-water blue-green algae.



THE THALLOPHYTES

If the schizophytes seem to stand at the very threshold of life, and to be sometimes scarcely distinguishable as either animals or plants, this can scarcely be said of the next main group, the phylum *Thallophyta* (Gr. *thallos* = young shoot). For most of these are definitely plants, though some still move independently, as animals do. In general they are not sharply differentiated into distinct units such as roots, stem, and leaves, but consist of a single undifferentiated body, a thallus. Moreover, they are so widely varied that at first glance many of them seem scarcely related at all. Just for this reason they are of special interest, for this one phylum, and more particularly one subphylum, the Algae, show the beginnings of sex and sexual differentiation, of cellular differentiation, and the gradual development from single-celled organisms through colonies to multicellular organization.

Sexual Reproduction

Reproduction is one of the most basic and important of all the processes of living organisms. In its simplest form, reproduction in typical cellular organisms is by mitosis. In the algae, a startling supplementary process is first introduced, for here we find plants suddenly producing special cells in a hitherto unheard-of way. Instead of simply growing up into duplicates of the plant which produced them, these special cells fuse, two by two, even to their nuclei. This process is sexual reproduction, and the fusing cells are gametes.

We at once tend to identify these gametes as sperm and egg cells. But in their simplest and most primitive forms, the two gametes may be completely alike in size and shape. Since the term *sex* is properly defined as the *difference* between the germ cells, or between the individuals engaging in sexual reproduction, we may say that obvious sexual differentiation is not an essential feature of sexual reproduction, but is rather a refinement or outgrowth of it.

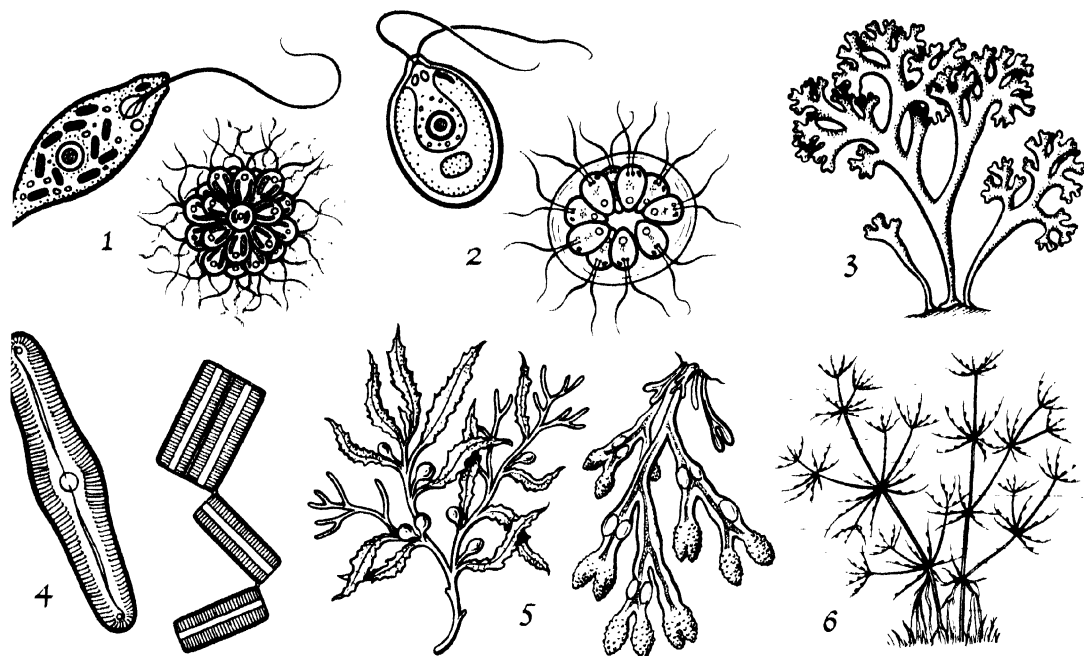


Fig. 118. Representative algae. 1. *Euglena viridis*, a common flagellate. *Synura*, a colonial form, annoys by imparting cucumber flavor to drinking water. 2. *Chlamydomonas*, a motile single-celled form; *Pandorina*, a motile colonial form. 3. *Chondros crispus*, a "sea moss" (red alga). 4. *Pinnularia*, a typical diatom; a colonial type. 5. *Sargassum*, the gulf weed, forms major part of vegetation in the Sargasso Sea; *Fucus*, the common rock weed of the seashore. Both are brown algae. 6. *Nitella*, common in ponds, a stonewort.

What really happens in this process of cell fusion called sexual reproduction? Why should such a process be substituted for the simple and apparently quite effective method of mitosis? And why should a differentiation between cells participating in fusion — that is, sexual differentiation or sex — be introduced into the already complicated process?

Chromosomal Events: Haploidy and Diploidy

There are reasonably satisfactory answers for all these questions, and, indeed, the fact that we can ask them in such a sequence is already an indication of our understanding. First, what really happens in sexual reproduction? By a specialized process of cell division called *meiosis*, in contrast with *mitosis*, gametes are produced which contain but a single full set of chromosomes instead of the double set present in the cells which produced them. We can verify this by looking at the process under the microscope. This shows us that the un-
mated or unfertilized egg contains one of each

kind of chromosome characteristic of the species, as does the male or sperm cell, while the fertilized egg or zygote contains two such sets, the egg set and that of the male cell which has fused with it. We say that the gamete has a haploid ("single") set of chromosomes, or simply that it is haploid, while the zygote is diploid ("double"). Since in most organisms subsequent cells are derived from the zygote by mitosis, these too are diploid. Hence the sexually produced organism is diploid, and if it is multicellular, so are all the cells in the body.

Since this diploid organism produces haploid gametes again, the diploid number must somehow again be reduced to the haploid. This occurs by a sequence of two cell divisions referred to as *meiosis*, or often, as the *maturation divisions*. In animals, meiosis generally occurs just before gamete formation, while in plants it occurs characteristically in the formation of spores. The process involves division of a diploid cell into four cells, each of which gets just

one set of chromosomes. In algae and higher plants, these haploid cells multiply to constitute the body of the next generation, which eventually produces haploid germ cells. In animals and all plants the haploid germ cells become diploid again when they fuse to make a fertilized egg, or zygote.

The Function of Sexual Reproduction

The obvious function of reproduction is to produce more members of the species. But the central fact of sexual reproduction, the fusion of gametes, is in a sense antithetic to reproduction, for the process yields fewer cells, not more. The reason for this must be a very important one, since most organisms reproduce sexually. In a keenly competitive world, sex can hardly be an idle luxury, but must offer vital advantages.

The answer lies in the behavior of the chromosomes. In asexual reproduction, the offspring produced by mitosis are exactly like the parent cell, unless a mutation occurs. All contemporary individuals are completely isolated genetically, so that there can only be divergence, never a pooling or sharing of new genetic acquisitions. Mutations occurring in different individuals in a population of such organisms can never be combined but go their separate ways in separate strains.

The sexual process completely alters the picture, for mutation A in one individual may now combine with mutation Z in another, and the characteristic AZ may be much more than merely the sum of the two factors. As a hypothetical example, a series of mutations may produce a reinforced jaw in one organism. In another, tooth-like structures may appear. Neither is very effective without the other. But the sexual process makes possible the combination of the two, thus by new combinations of mutant genes producing something entirely new and different, and more advantageous than either alone.

The advantage of sexual reproduction may be stated briefly thus: sexual reproduction increases the heritable variability of organisms.

Again we may be reminded that change is not synonymous with improvement, but obviously improvement is impossible without change. Since heritable variation is one of the cornerstones of evolution, sexual reproduction accelerates evolution. It must not be thought that sexually achieved recombinations are necessarily good. Some may be very bad. But natural selection strikes out the unhappy combinations while it preserves those which represent an improvement.

Sexual Differentiation of the Gametes

Since sperm and egg are gametes, there is a tendency to think of all gametes as male and female, that is, as sexually differentiated. But as we have said, the simplest sexually reproducing algae are, according to our accepted definition of the word, neither male nor female, both uniting gametes being apparently alike. This makes the origin and evolution of sexual reproduction and sexual differentiation much more understandable. It is remarkable that organisms still live today that have preserved some of the possible steps in the transition from simplest, non-differentiated sexual reproduction up to the most complex sexual differentiation.

Why should sexual differentiation have evolved? Where and why did it begin? We know that it evolved very early, and the reason for it may be found in the functions that gametes must fulfil. For successful sexual reproduction, it is first necessary that the two gametes meet; then, having met and fused, they must have enough reserve food energy to establish a new organism. In other words, gametes should be motile and they should carry a reserve food supply. But food storage and motility conflict. Picture the difficulty a hen's egg would have moving about the barnyard in search of a sperm! The two demands have been met by specialization in each gamete for one of these two functions. The sperm cell becomes motile while the immobile egg specializes in food storage. It is from these needs that specialization into male and female arose.

Sexual Differentiation of the Organism

In the meantime multicellular organisms had evolved — a long story in itself — and gradually the sexual specialization first appearing in the gametes carried over to the gamete producers, so that one eventually became limited to the production of male gametes and another to female. All this, too, can be traced in the algae.

The advantages of this specialization appear at once. First, it eliminates the mating of gametes from the same parent and thus prevents genetic isolation. If the main advantage of sex is the spread of variation, sexual differentiation in the parents makes this increasingly possible. Second, it makes possible the advantage of further specialization of each sex so as to further the function of its germ cells. In higher animals the two sexes have developed highly specialized organs to produce and spread their germ cells. Thus sex, or sexual differentiation, at first a specialization of the gametes, has reached over to the gamete producers.

The Multicellular Organism

A study of the algae will also enable us to piece together the evolution of single-celled organisms into multicellular ones (Fig. 119). The story is not altogether simple and clear, for a multicellular organism is far more than the sum of its parts — more than a mere collection of cells. It is certainly nothing less than miraculous that a single cell, such as a human zygote, should produce a coordinated body of billions of cells. How did such changes ever come about? What advantages — and what disadvantages — accompanied them?

The first step appears to have been the establishment of colonies, groups of cells in place of single or separate ones. In the simplest colonies all cells are alike and there is no division of labor. But mutations brought about some form of differentiation, which apparently improved efficiency and so had selective value. Thus certain cells of the colony became more efficient eaters, others more efficiently motile, and so on.

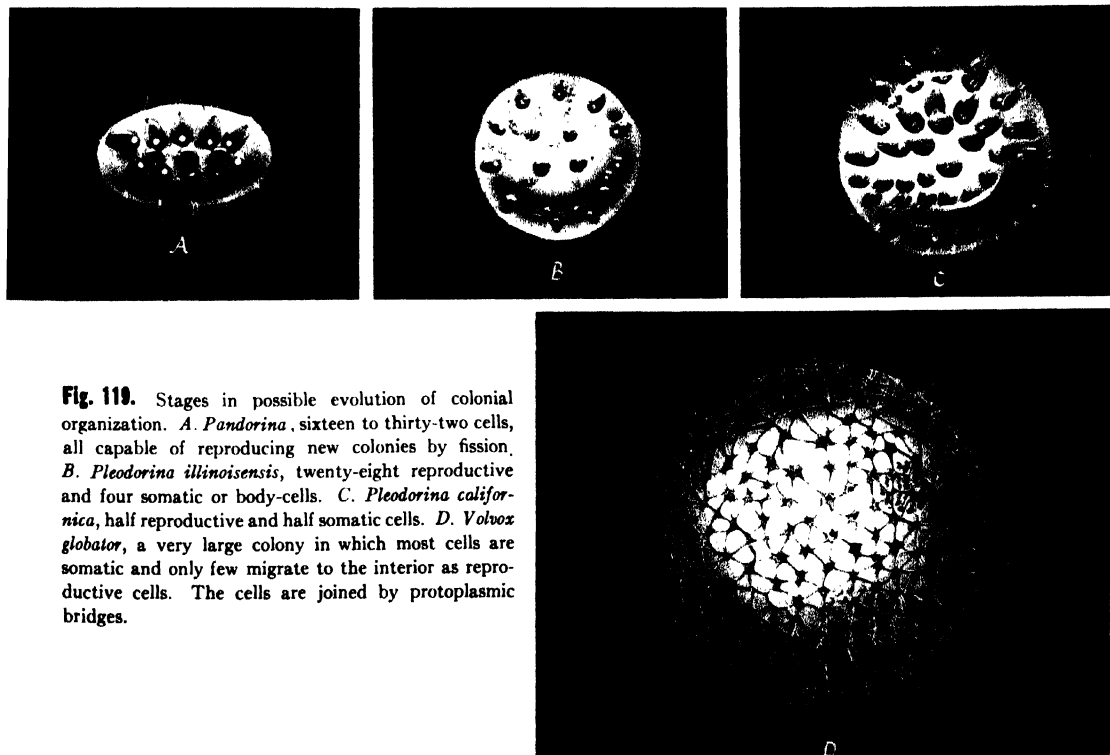


Fig. 119. Stages in possible evolution of colonial organization. A. *Pandorina*, sixteen to thirty-two cells, all capable of reproducing new colonies by fission. B. *Pleodorina illinoisensis*, twenty-eight reproductive and four somatic or body-cells. C. *Pleodorina californica*, half reproductive and half somatic cells. D. *Volvox globator*, a very large colony in which most cells are somatic and only few migrate to the interior as reproductive cells. The cells are joined by protoplasmic bridges.

The advantages of colonization and later cellular differentiation are obvious. Only in a united group may a cell become a one-sided specialist and still survive, for only then would others, profiting by its specialty, repay their debt by supporting it. Thus cells specialized as locomotors would be fed by others. When such a state of specialization and interdependence is attained, we no longer speak of a colony, but of a multicellular organism. Such organisms have attained immeasurably greater mastery over their environment, in greater motility, less vulnerability, and far finer adjustment.

Physiological Death

These benefits were not purchased without a price. As the colonies became multicellular organisms and interdependence increased, a new phenomenon, physiological or "natural" death, made its appearance. Among the simpler creatures which reproduce by mitosis and thus each time become two new, young cells, no corpse is left, and no cell has been destroyed. There is no "natural" death. In the entire direct ancestry of such an organism no death has ever occurred, either natural or violent, for if it had, the line of succession would have been broken, and the present cell could not exist. The statement that simple organisms are potentially immortal is startling only because we and most creatures we see are not. It appears that natural death did not exist until specialization began. In a sense, therefore, death may be considered a penalty for specialization.

A technique of growing the tissues of organisms in sterile glass containers sheds some light on this theory. In 1907 R. G. Harrison showed that it is possible to grow cells from the tissues of organisms in special nutrient media outside the body. The method was gradually improved until today almost any tissue can be grown almost indefinitely in a culture flask. Cells from the heart of an embryonic chick were so cultured for over thirty years by Alexis Carrel. An ordinary chicken, on the other hand, will, if it escapes the pot, live about a dozen years. In time its tissues show changes in structure

and behavior characteristic of senescence, and not long thereafter it dies of old age. But the cells from the embryonic chick heart show no signs of age as long as the medium in which they are cultured is frequently changed, and as long as the tissue is pruned to keep it from growing too big, although they have been kept functioning for well over twice their normal life-span. Tissues from the bodies of other animals and of human beings have responded similarly. From this we can reasonably conclude that, for some reason, life within the community of cells which makes up a multicellular organism appears to be less healthy or less conducive to longevity than life in a tissue culture. Further, these experiments imply that the cells of multicellular organisms have not lost their potential immortality at all, but rather that senescence is somehow a result of regimentation within the organized community of the body. Perhaps aging is merely an indication that the chemical coordination between the cells of the body is less than perfect, that the multicellular organization has attempted more than it can fully achieve, and that each cell, dependent on the environment created by all the other cells of the organism, does not have an ideal medium for nourishment and elimination. If so, we may conclude that death is the price which the multicellular organism has paid for increasing specialization and increasing control over its external environment. Further, it is not impossible that chemists and physicians may some day solve the problem of chemical balance within the body and again endow it with potential immortality.

The Thallophytes: General

The group consists of two subphyla, the Algae (L. *alga* = seaweed) and the Fungi (L. *fungus* = mushroom), though not all algae are seaweeds nor all fungi mushrooms. Indeed, the group is quite diverse in both structure and behavior, and certain organisms do not fit precisely into either division. Thus the plasmodium, which is considered a fungus, shows characteristics of certain bacteria and of certain ameboid protozoa as well as of the flagel-



Fig. 120. *Euglena viridis*.

lates and of the fungi. In short, the phylum is a sort of catch-all for simple plants, and most of the principal types may be regarded as individual developments in distinct and random directions. At the same time, similar developments often arose independently and repeatedly in organisms not closely related. Perhaps the most surprising feature of the group is that so many different experiments were successful enough to survive, and that some of them, such as certain parasitic fungi, have persisted for several hundred million years almost unchanged.

Some thallophytes are unicellular, some occur in aggregates of like cells, and some, with cells that are considerably differentiated, are multicellular. Others consists of a continuous protoplasmic mass called a syncytium, containing many nuclei not divided into separate cells. All thallophytes, however, have distinct nuclei, and most have some form of sexual reproduction. In some, the pattern of reproduction is extraordinarily complex, though in others the sexual mechanisms are remarkable degenerated. In short, almost the only common characteristic of the group is that it is generally primitive.

THE ALGAE

There are six main classes of algae, ranging from the primitive flagellates, single-celled creatures which propel themselves through the

water by whip-like flagella, to the stoneworts, brittle and slender green plants that look like miniature aquatic Christmas trees.

These minute creatures are of interest mainly because the more primitive ones show characteristics of both plants and animals. They are of many varieties and habitats, some existing in fresh water ponds, while others are found in many environments and some are parasites. Some contain chloroplasts and are green, and as the presence of chlorophyll would suggest, are capable of photosynthesis like other green plants. These are holophytic in metabolism. Of this type is (*Euglena viridis*, Fig. 120). Other species, almost identical in form, lack chlorophyll and are typically holozoic, ingesting solid food particles as animals do. In this group is *Trypanosoma gambiense*, cause of the deadly African sleeping sickness. Thus the flagellates may be considered as the archetypes of primitive animals as well as of plants. There are still other connections between the flagellates and other simple organisms. The syphilis germ, the protozoan-like bacterium *Treponema pallidum*, looks and behaves somewhat like a flagellate. The group seems to stand at the threshold of differentiation, and its place in the evolutionary story is blurred and uncertain.

Euglena is typical in its curious blend of animal and plant. This small, blimp-shaped organism, with a single flagellum at its head

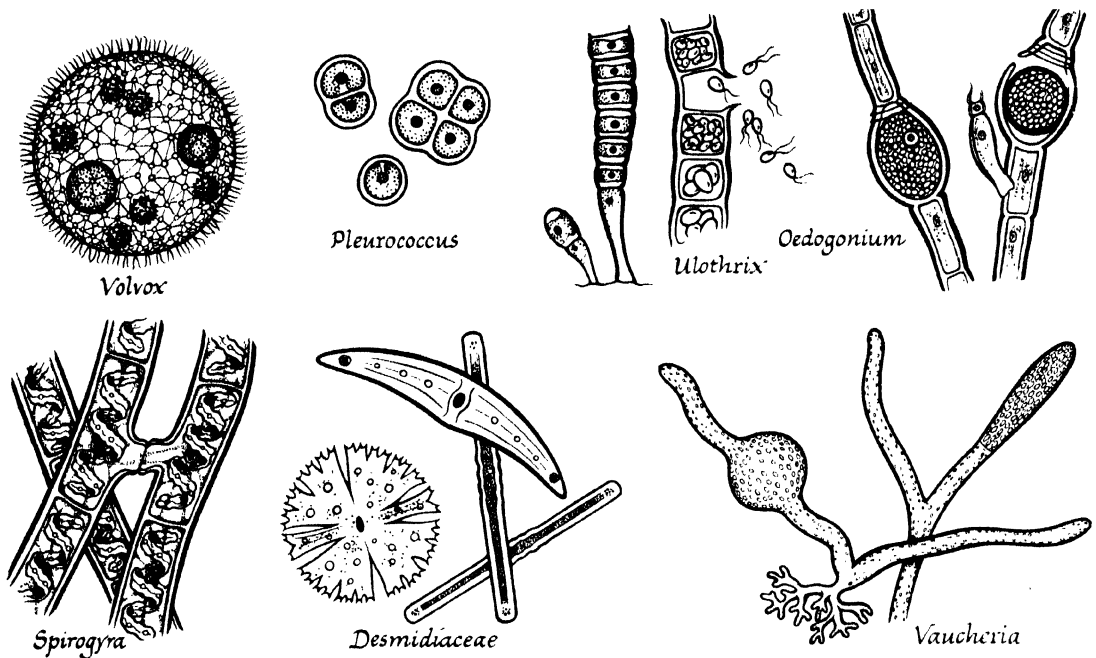


Fig. 121. Representative green algae. *Volvox*, a complex colonial form on the verge of becoming multicellular. *Pleurococcus*, imparts a green hue to the bark of trees. *Ulothrix*, the filaments form a plushy coating on rocks in springs. *Oedogonium*, also filamentous, attached or free-floating. *Spirogyra*, the common pond scum, or pond silk. Desmids. *Vaucheria*, forms felt-like masses in streams and greenhouses.

end, may be found in almost any sample of summer pond water. It retains its shape by virtue of a thin pellicle or outer sheath surrounding the plasma membrane and sufficiently elastic to permit considerable change of shape as the organism squeezes its way between the threads of other algae. It usually moves about very actively. At the base of the flagellum is a red eye-spot which appears to be sensitive to light, thus enabling *Euglena* to orient itself with respect to light and dark. In these respects it is extraordinarily like an animal. Because of its numerous green chloroplasts, it can manufacture its own carbohydrates, but in the absence of light it can also absorb organic molecules from its surroundings. Thus, unlike most plants, it may engage in true heterotrophic metabolism. Reproduction occurs by longitudinal rather than transverse fission. *Euglena* shows no trace of sexual reproduction.

The Green Algae

More important to our story than the flagellates is another class, the Chlorophyceae (Gr.

chloros = light yellow-green), or green algae, which show the beginnings of sexual reproduction and the first steps toward cellular differentiation (Fig. 121). Of these one order, the Volvocales (*L. volvere* = to roll), allows us to reconstruct the whole process of evolution from single-celled to multicellular as well as the first important steps in the evolution of sexual reproduction. The Volvocales are flagellates like *Euglena*, but each cell has two whips instead of one. While all are motile, some are single-celled, some colonial, and some on the verge of being multicellular. All have chloroplasts.

Sexual Reproduction Typical of the group is *Sphaerella* (Fig. 122), a small unicellular creature characterized by the red coloring-matter it produces. Ordinarily, under favorable environmental conditions, *Sphaerella* reproduces asexually by passing into a non-motile resting stage, during which the nucleus divides repeatedly and produces four to sixteen haploid daughter cells, which eventually rupture the wall of the old cell and escape. These daughter

cells are called *zoospores*, that is, they are unicellular asexual reproductive bodies which are motile, like animals. They may remain in this stage for some time, actively carrying on metabolism and increasing in size. But sooner or later they repeat the process of division, though with slight modifications, while the red coloring-matter diminishes and is replaced by chlorophyll. Thus new individuals develop.

With unfavorable nutrition, however, the reproductive behavior of *Sphaerella* changes, and the organism exhibits simple aspects of the sexual process. Less robust daughter cells are produced, and these behave like gametes, since they are generally incapable of producing new individuals unless they unite in pairs. This difference in behavior is not clearly understood, but it appears to be due to some lack in the composition of gametes which normally is remedied only by fusion or experimentally by suitable nourishment.

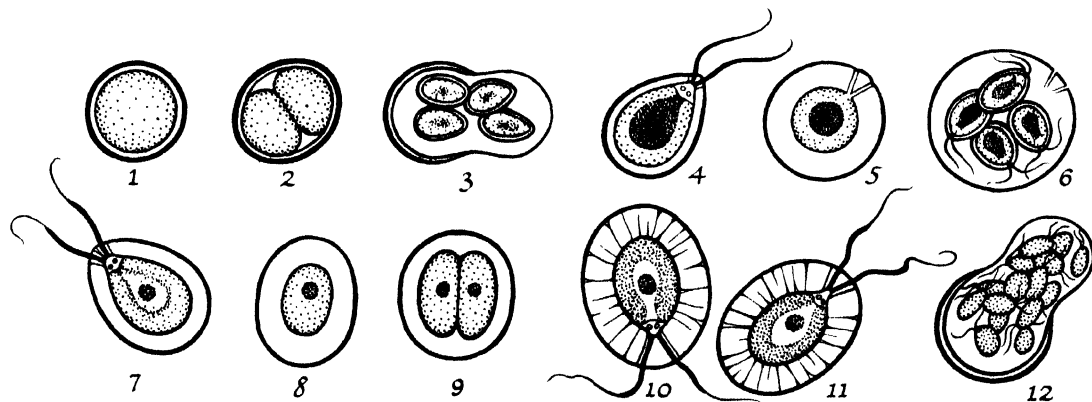
In *Sphaerella* the gametes are similar to zoospores in that they are free swimming haploid cells, but they are produced in larger numbers and can usually grow into normal adults only through union. Unlike the more highly developed gametes we shall see later, these are not visibly distinguishable as male and female forms. Sexual reproduction of this kind, in which the gametes are not differentiated, is known as *isogamy*. It is safe to assume that

this is a fairly primitive stage in the development of the sexual process.

Observation of other members of the Volvocales bears out this conclusion. *Chlamydomonas* (Fig. 123), a genus closely related to *Sphaerella*, also generally reproduces by the fusion of two like gametes, though in some others of the Volvocales the gametes are differentiated into male and female and are unequal in size, the latter being slightly longer. Other types show increasing differentiation in the gametes, and finally *Volvox* (Fig. 119) is *oögamous*; that is, it has true eggs and sperms. Here the female gamete, or ovum, is large as cells go, is immobile, and is packed with reserve food materials, whereas the sperm cells are minute, and in extreme cases are nothing more than highly mobile parcels of genes.

Cell Specialization. The Volvocales also show the first stages in another momentous development: cell specialization, which ultimately produced such highly specialized types as bone, brain, and muscle cells. Many of the gametes and zoospores of the thallophytes, and even of higher plants, are motile, like the sperm cells of animals. In *Sphaerella*, and others, the non-motile phase is merely an interlude between motile zoospore stages. But the fact that both types exist in the life cycle of the same organism is a step toward cell specialization.

Fig. 122. Life-history of *Sphaerella*. 1. Resting stage. 2, 3. Divisions. 4. One of the escaped cells, a zoospore of the first generation. 5. Zoospore at rest. 6. Forming four new zoospores. 7. A zoospore of the second generation. The red material (shaded) is reduced. 8. Third resting stage. 9. The cell dividing. 10, 11. Zoospores of the third generation with distended cell wall and small red area. Protoplasmic strands connect the cell-body with the surface. 12. Resting cell dividing into small zoospores.



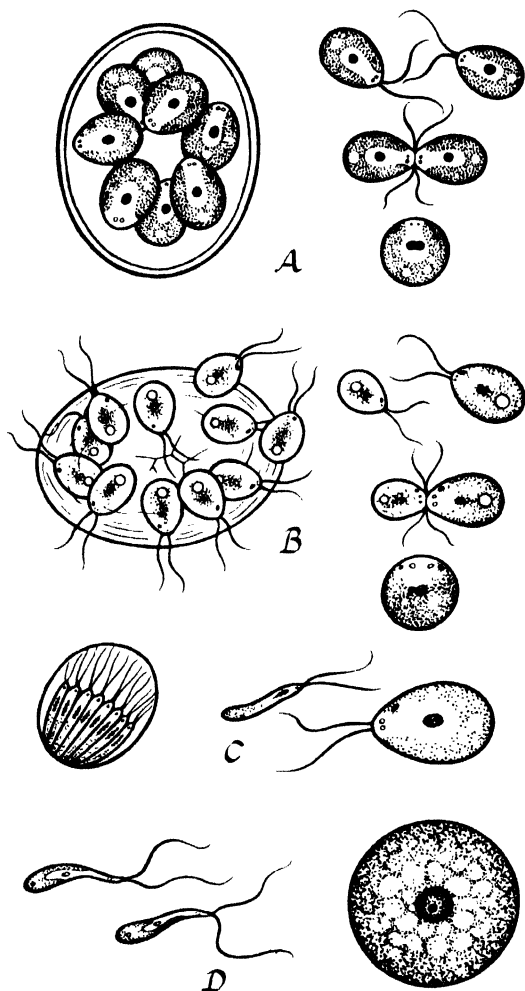


Fig. 123. Progressive stages in sexual differentiation. *A. Chlamydomonas*; formation of gametes and fusion of physically similar ones from different colonies. *B. Pandorina*; liberation of gametes and fusion of dissimilar ones. *C. Eudorina*; gamete formation, micro- and macrogamete. *D. Volvox*; microgametes now sperm cells, and macrogamete, egg cell.

The next big step is the development of plant colonies (Fig. 119). While some species of *Chlamydomonas* are unicellular, others consist of cell aggregates. *Pandorina*, for instance, is a colony of about sixteen cells, all practically indistinguishable in form and structure. Each cell is flagellated, and each carries on all the essential life functions, although such cells never appear singly except as gametes. Other members of this group, such as *Eudorina* and

Pleodorina, form much larger colonies, until in *Volvox* the colonies may contain as many as twenty thousand individual cells.

As the size of the colonies increases, they tend more and more to produce two types of cells instead of one: germ cells, which retain their capacity to reproduce new individuals, and somatic cells, which are smaller and do not. Both retain flagella and motility. Thus in *Pleodorina illinoiensis*, the majority of the cells are flagellates of the same type as all those in the simpler *Pandorina* colony, and all can reproduce. But a few of the cells are smaller and also are physiologically different. For when the colony multiplies, the smaller somatic cells are unable to participate. Here, then, for the first time there appears the differentiation between *germ* or reproductive cells, and *body* or *somatic* cells. In this species the former far outnumber the latter, but in another variety of *Pleodorina*, the two types are almost even in number. In the comparatively immense *Volvox* colonies there are relatively few germ cells. Thus in three stages in the growth of specialization, each successive stage shows the reproductive function limited to a smaller and smaller proportion of the total organism.

It is interesting to note, also, that *Volvox*, the most advanced in this trend, has differentiated male and female gametes, and in addition shows a third step toward more highly organized life forms. When the new colonies are produced, the old one is ruptured while they escape from it and leave it to die. Sex, cell specialization, and death all appear in one small group.

Simpler Green Algae. Another type of green algae, the order *Chlorococcales* (*Gr. chloros* = yellow + *kokkos* = seed), shows other interesting advances in the direction of plant specialization, though its members are more primitive in reproduction and cell specialization. Typically, these are simple, spherical green cells. Some of them live in moist shady places on land, unlike most algae, and some are symbiotic — that is, they live in a relationship of mutual dependence and advantage with some other type of organism.

The common *Pleurococcus* is the plant usually responsible for the green tinge on the shady side of tree trunks, especially conspicuous after a rain. Ordinarily it reproduces by mitosis, since in the conditions under which it generally lives, swimming spores or gametes, such as those of *Sphaerella*, could not function. Under conditions of increased moisture and higher temperature, however, *Pleurococcus* forms motile zoospores similar to those of *Sphaerella*. Also in this organism the relation between the motile and non-motile phases is opposite to that in *Sphaerella*, for in *Pleurococcus* as in most higher plants it is the normal rather than the reproductive phase that cannot move.

Among the members of this group which are symbiotic is *Chlorella vulgaris*, which is similar in appearance to *Pleurococcus* and frequently lives intimately lodged between the cells of simple animals such as the *Hydra* and the *Planaria* or between the cells of fresh water sponges.

A similar plant is the green element in lichens (Fig. 124), examples of which are the gray-green leathery plants often seen growing on rocks. The unusual feature of lichens is that they are not single plants, but each lichen is really two — a green alga, related to *Pleurococcus*, living in symbiosis with a colorless fungus.

Lichens have an unparalleled ability to grow in seemingly impossible places, on bare rocks in the blazing sun, on seashore boulders, on the bark of trees, or festooned from their branches as in "old man's beard." Their ability to endure cold makes them the dominant vegetation in such regions as Iceland and Greenland. Lichens are plant pioneers, through their astonishing ability to endure extremes of temperature and drought. Much of the earth would still be a barren waste of rocks and boulders and sand, but for the foothold given to other plants by lichens. The fungus member of the partnership forms a dense web of threads (*mycelium*) within which the algae lie protected. The fungus threads penetrate even the rock, and cling tightly. They absorb salts from the

rock and water from the air or from occasional showers, and they store it. (In exchange for sugar obtained from the photosynthesizing algae, they provide them with water, salts, and protection.) Neither member of the partnership could survive alone in most of the regions where lichens thrive.

Definite Plant Forms. A third order of the green algae, the *Ulothricales* (Gr. *oulothros* = woolly-haired), shows marked advances both in cellular specialization, which has by now produced a multicellular structure in the plant, and also in the reproductive process. These plants may have the form of filaments, that is, threads composed of a number of similar cells, as in *Ulothrix*; or they may form large, flat sheets, as in the sea-lettuce, *Ulva*. In the *Ulothrix* filament, which is non-motile, the cells distinctly show the beginning of differentiation, since a few cells at the base of the thread are colorless and serve only to hold the organism

Fig. 124. "Reindeer moss," *Cladonia*, a lichen forming clusters of gray coral-like growths.



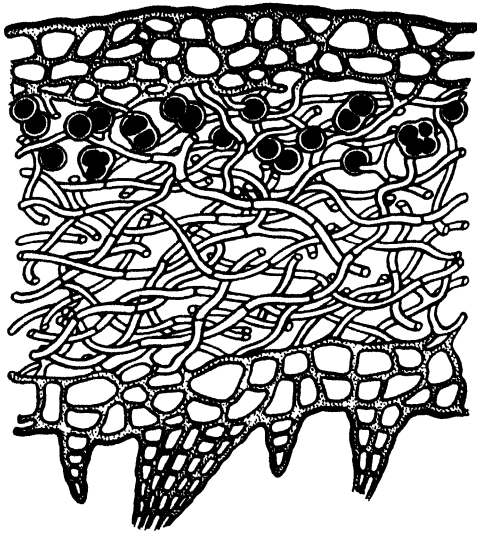


Fig. 125. Section of a lichen, showing felt-like mycelium of fungus with alga cells nested in it.

in place on the rock on which it grows. The remaining cells are green, contain chlorophyll, and serve for photosynthesis. In *Ulva* the cells form large sheets consisting of two layers, and look somewhat like lettuce — hence their name. Here again there is a differentiation between colorless “holdfast” cells and the rest of the plant.

Ulothrix and Alternation of Generations. Important as these beginnings of cellular differentiation are, *Ulothrix* is of greater significance to us because here there are to be found certain basic changes in mode of reproduction which represent the beginnings of a complex cycle found in all higher plants. We refer to this reproductive cycle as an alternation of generations, because two differently shaped and constituted forms of the plant actually do alternate in successive generations of the reproductive cycle. Since *Ulothrix* does not yet show this system distinctly, a glance first at the much more highly differentiated fern-plant will help to illustrate the general features. When a fern-plant reproduces, it releases small cells called spores. These fall to the ground, germinate, and grow into a new multicellular plant. This new plant, however, is totally unlike the fern plant which produced the spores, for it is merely

a heart-shaped thallus, half the size of a dime, and this in its turn produces gametes instead of spores. When two gametes unite, they also develop into a multicellular plant, but this time the plant is again a typical fern. Thus two distinct generations, differing in structure and function, alternate in the reproductive cycle. *Ulothrix* illustrates the beginning of such a cycle (Fig. 126).

Under certain conditions of temperature, chemical composition of the surrounding water, and internal state of the plant, *Ulothrix* cells in a filament may divide into two or more cells, each with flagella. These cells thereupon escape through the ruptured wall and swim away. Each then gives rise to a new filament by cell division. This method of reproduction is strictly asexual and shows no alternation of generations. Under different conditions, usually unfavorable, the filament cells divide into large numbers of smaller cells, also flagellated, which likewise escape from the ruptured cell.

These cells, though first and foremost gametes, may also behave as zoospores in case they should fail to find a partner. It must be noted, however, that the filaments produced from such unsuccessful gametes, or small zoospores, are also smaller and relatively feeble. There is no noticeable difference between the gametes, but gametes from the same filament will not fuse. Hence *Ulothrix* is *heterothallic* (*hetero* = different + *thallus*). This mode of sexual behavior indicates that there must be some difference between the two gametes, even though none is visible. So this condition provides a gradual transition between *isogamy* and *anisogamy*, that is, a condition where there is a difference between the gametes.

The zygote does not at once continue its growth, but generally passes into a resting stage, after which it divides into a number of spores, each becoming a new filament by cell division. Here is a beginning of that alternation of generations. The original filament, though capable of reproducing asexually by spores, is also capable of producing gametes. It is therefore potentially a *gametophyte*, that is, a gamete-producing generation. The zygote

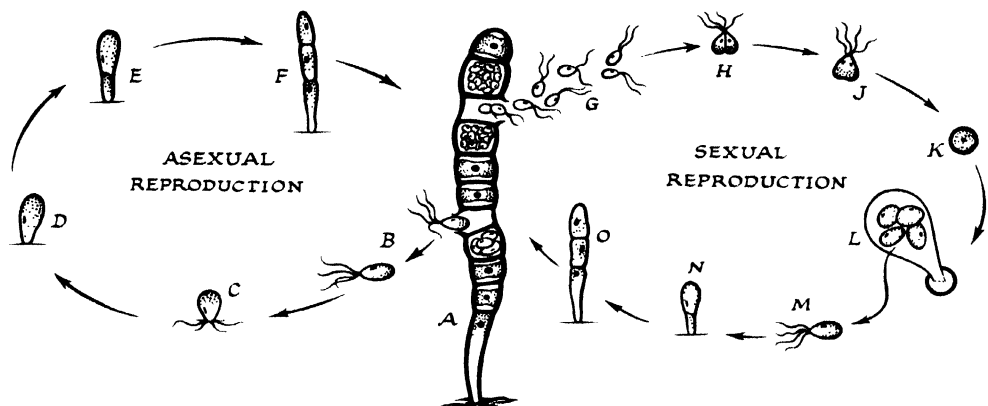


Fig. 126. The reproductive cycle of *Ulothrix zonata*. A. Portion of a filament showing spores and gametes. B-C. Spores. D-F. Growth of filament. In the sexual phase, H shows gametes (from different filaments) fusing; J-K, zygote; stages L-O, of germinating zygosporos.

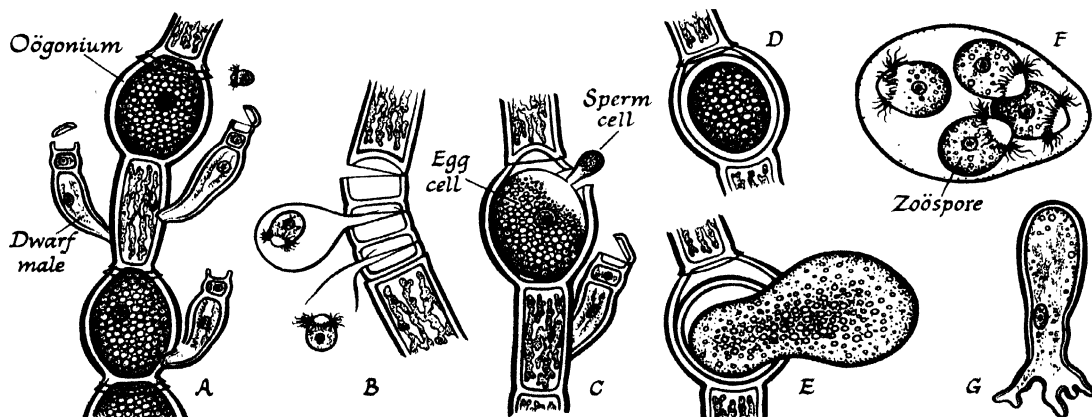
then becomes transformed into a multicellular mass of spores which may be regarded as a *sporophyte* — a spore-producing generation. To be sure, the sporophyte cells themselves become the spores of the following generation, but an alternation of generations is clearly evolving.

Sexual Differentiation. Still further sexual differentiation is found in another order of the green algae, the *Oedogoniales* (Gr. *oidein* = to swell + *gonos* = seed), small aquatic plants with the same kind of filament structure and habitus as those just discussed. Some produce branched filaments, while others have unbranched filaments similar to *Ulothrix*. *Oedogonium*, representative of this group, has a large reticulate chloroplast shaped like a hollow

cylinder. These plants are quite common in small bodies of fresh water and form green coatings over rocks and other objects.

Oedogonium ciliatum (Fig. 127) displays two advances in the reproductive processes. Like *Ulothrix* it has an alternation of generations, but it also shows a considerable advance in the differentiation of male and female gametes. As in *Volvox*, the female gamete, the ovum, is quite large, since it is heavily stocked with reserves of food, and is non-motile, whereas the male gamete, the sperm cell, is small and highly motile. The gametophytes also are differentiated into male and female types. In *Oedogonium* the female gamete is produced singly in any one of the cells of a female fila-

Fig. 127. *Oedogonium* life cycle. A. Mature female filament with oogonia and attached dwarf males. In this species, males are from spores produced in another filament. B. Male filament; small cells producing androspores, which produce dwarf males. C. Oogonium at moment of fertilization. D. Ripe oospore. E. Germinating oospore. F. Four zoospores formed from escaped contents of oospore. Each can grow directly into a new filament (G).



ment. The male gamete is produced in a more complex manner, but arises indirectly from cells of another filament. Ciliated spores are released from the male filament and swim about until they meet a female filament. Here they settle, sometimes on the oogonium itself, and develop into a reduced or simplified filament, called a dwarf male. This is a highly specialized male gametophyte, and it produces sperm cells which now enter the oogonium and fertilize the ovum within it. The spermatozoa are released through a small trapdoor at the top of the dwarf male. This is not only sexual reproduction, but a differentiation into male and female plants and gametes.

Chemical Differentiation of Gametes. Another order of green algae, the *Conjugatae* (L. *conjugare* = to unite), show a difference in the behavior of gametes but not in their form. The common pond scum, *Spirogyra*, is typical of the order. Unattractive as its green, slimy masses look when fished out of the water, the individual plants when viewed under the microscope are beautiful in form (Fig. 121). Colonial organisms consisting of unbranched filaments, they are characterized by elaborate chloroplasts which consist of one or several spirally wound ribbons with scalloped edges, lying just inside the cell membrane of each cell. A thin film of cytoplasm forms the protoplasmic medium in which the chloroplasts are maintained. The whole inner region of each cell is a vacuole devoid of protoplasm except for an island of cytoplasm at the very center, within which lies the nucleus. Thin, mucilage-like threads of protoplasm connect the nucleus with the peripheral film of cytoplasm. These cells lie end to end in long, slender filaments much finer than a hair.

Unlike the other algae so far discussed, the *Conjugatae* reproduce only sexually and whole cells act as gametes. While there is no difference in the form of the gametes, there is a marked difference in behavior, for those produced in one filament are active while those in the other are passive receptors.

In *Spirogyra*, two adjacent filaments develop snout-like protuberances on each cell on the

side facing the opposing filament. The protuberances eventually meet and fuse, forming bridges between the two strings of cells. There is no perceptible difference in shape or structure between the cells in the two filaments; yet the events that follow indicate that there must be a physiological difference, for one of two joined cells begins to shrink away from its cell wall and to flow through the connecting tube into the interior of the other cell. Nor does this appear to happen by chance, for the cells which migrate are always from one filament and those which receive them are always in the other. The cells of the active filament are termed male; those of the passive one, female. Like *Ulothrix*, *Spirogyra* is heterothallic. Numerous modifications of this process may be found among other *Conjugatae*.

Other members of this order, the *desmids*, are unicellular, and are noteworthy chiefly for their beauty and symmetry (Fig. 121). They rarely form colonies or threads, though their reproduction is similar to that of *Spirogyra*.

Finally, among the green algae there is the order *Siphonales* (Gr. *siphon* = pipe), which has reproductive processes like those in some of the forms already discussed, but exhibits a peculiar tube-like multicellular structure. *Vaucheria*, a representative of this group, forms the felted green masses often seen on flowerpots in greenhouses. The plant consists of long hollow threads, lined on the inside with a continuous film of cytoplasm containing many nuclei, but it is not divided into separate cells. Its zoospores, like the plant itself, are multinuclear, and actually represent a unified mass of many zoospores. The male and female *gametangia*, those bodies which produce the gametes, are formed on adjacent portions of the same filament. It is difficult to see what advantages the sexual fusion of gametes produced by the same filament can bring with it, but a study of genetics shows that there are some, even though slight in degree.

Thus the Chlorophyceae is seen to be a remarkably interesting group, for varied as the green algae are, they show the beginnings of sexual differentiation not only among their

gametes but also in the plant body, and they also show marked development in cell specialization.

Other Algae

The Red Algae. The four other types of algae may be mentioned more briefly. The red algae, ranging in color from red to purple, are much more highly specialized than either the simple flagellates or the green algae, for they consist of a root-like base which anchors them to rocks and similar objects, and a complicated body, which may take the form of a many-branched stem or of a leaf-like structure with a central stem. Although these plants show considerable complexity, they are not otherwise important in the evolutionary story, since they are not ancestral to any higher plants with the possible exception of some of the higher fungi. They have some commercial importance, however, since they are used in agar, a gelatinous substance used in jellies and ice creams and as a culture medium for bacteria.

The Diatoms. These minute organisms are single cells or colonies of a yellowish brown, and are of particular ecological importance because of their great numbers and wide distribution. Diatoms form the brownish coatings often seen on objects floating in ponds and streams, and they are an important part of the ocean plant life which floats freely in the water and is termed plankton. Through their photosynthetic activity, in which oils rather than carbohydrates are formed, they provide great quantities of organic food matter for other life forms. Plankton, eaten by small marine shrimps which in turn are eaten by larger animals, is the ultimate food source for nearly all marine life. Diatoms are peculiar in that their protoplasm is surrounded with glass-like silicious skeletons which are almost indestructible. This material, known as *diatomaceous earth*, is found in vast deposits in many parts of the world and serves a variety of industrial uses, in scouring powder, as a filtering medium for liquids, and in other ways. Seen under the microscope, the diatoms' peculiar box-shaped housings are of extraordinary beauty, showing delicate tracer-

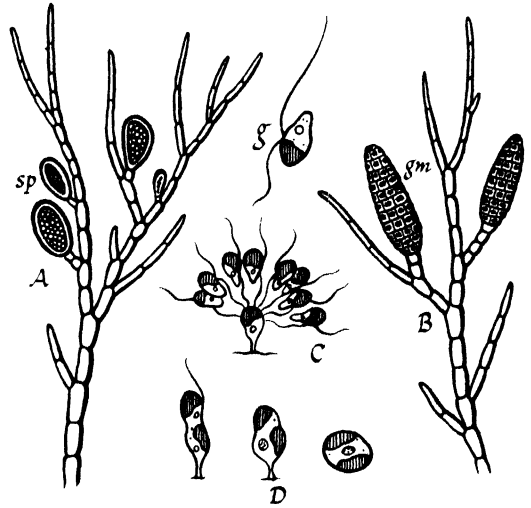


Fig. 128. Reproduction in *Ectocarpus* (brown algae). A. Branched filament with several sporangia (*sp*); *g*, zoospore. B. A branch-bearing gametangia (*gm*). C. Non-motile female gamete surrounded by motile male gametes. D. Fusion of gametes, with zygospore (right).

ies of etched patterns (Fig. 118). Many ancient, fossilized forms are almost identical with those of today. Reproduction in these plants is both sexual and asexual, the former isogamous.

The Brown Algae. Largely salt water plants whose pigmentation frequently conceals chlorophyll, these are multicellular, and, like the red algae are usually more highly differentiated in structure than green algae. A common variety is the ordinary rock-weed, *Fucus*. This is an olive-green branching plant which occurs in vast, dense masses attached to rocks below the high water mark. The body of the plant consists of bifurcated, specialized branches which contain bladder-like, buoyant air sacs in matched pairs. Reproduction is sexual, and the male and female germ cells are usually produced on separate plants. The *Sargassum*, a graceful floating weed, forms dense masses of vegetation in the Atlantic, and the great bladder kelps of the Pacific are of interest because of their fantastic lengths, which may be as great as 900 feet. The latter are an important source of iodine.

The Stoneworts. Named for the lime deposits

in their cell walls, these are delicate plants, looking somewhat like miniature Christmas trees. Usually found in fresh water, they consist of slender cylindrical axial stems around which are arranged whorls of short leaf-like branches. The cells are all green and contain numerous chloroplasts, as in *Nitella* (Fig. 118). This group is sharply isolated from all other algae, and it is sometimes questioned whether it belongs with the algae at all. Stoneworts show considerable differentiation and specialization in their body structure, for they have stem-like and leaf-like as well as root-like anchoring cells. The stem of the plant consists of a hollow cylindrical structure with a continuous lining of protoplasm in which there are numerous nuclei, much as in *Vaucheria* (see page 176). At the ends of these cylinders, called internodes, cells with single nuclei form a node, a sort of crown, from which lateral internodes, or leaves, originate. All the cells contain innumerable small spherical chloroplasts

affixed to the inner side of the cell membrane. The protoplasm is of unusual interest for microscopic observation because of the incessant streaming that can be observed in it. This may be considered a sort of specialization for the distribution of organic compounds within the plant. Apical cells at the ends of stems and branches may divide to form new cells of their own kind or to grow into specialized reproductive structures.

The algae are indeed a varied group, ranging from the one-celled flagellates, some of which show distinctly animal characteristics, to the clearly plant-like stoneworts, that possess the beginnings of roots, shoot, and leaves. And the complicated process of sexual reproduction has here made its appearance.

FUNGI

General Characteristics

The second subphylum of the thallophytes, the Fungi, is a large and varied group which includes such organisms as molds, yeasts, rusts, blights, mildews, toadstools, and mushrooms (Figs. 129 and 130). Some, like the yeasts, represent about the simplest form of cellular life. Others have developed a considerable degree of specialization. All the fungi are either saprophytic or parasitic, since all lack chlorophyll. In fact, the absence of chlorophyll is probably their most striking common feature. Despite the lack of nutritional independence which the absence of chlorophyll generally implies, the fungi appear to be a most successful group, since it is estimated that there are at least 100,000 species, and there is practically no spot on earth without them. First adapted to life in the water, or at least descended from aquatic forms, many of them have evolved changes in structure and behavior that now equip them well for land life. Geologically they are considered a very ancient group, and fossil plants found in Rhynie chert of the Devonian show traces of the delicate hyphae or threads of parasitic fungi.

The thallus of one of these plants may be either unicellular, or typically cellular, or syn-

Fig. 129. The edible morel, *Morchella*, a sac fungus.





Fig. 130. The oyster mushroom (*Pleurotus ostreatus*) and the common cultivated mushroom (*Agaricus campestris*).

cytial, that is, consisting of a mass of protoplasm with many nuclei but not divided into separate cells, and much like that of the green algae from which many of them are thought to have arisen. Typically, fungi develop as a complex mat or *mycelium* (Gr. *mykes* = fungus) of delicate tubular fibers called *hyphae* (Gr. *hyphē* = web), which grow and insinuate themselves into the matter, living or dead, which serves them for food. As they grow, the younger portions of the growing hyphae penetrate new areas and absorb available food, while the older parts of the mycelium become filled with absorbed food reserves. Under these conditions, in due time, new types of hyphae may develop with different habits and different functions. These form the reproducing bodies, or *sporangia*. It is these which the average person would recognize as a fungus, for they form the visible toadstool, mushroom, or bracket fungus, while the main body of the plant remains invisible within its host or under the ground, carrying on its function of absorbing food. This is why the removal of a mushroom does not destroy the plant. The mycelium can continue to live and eventually produce new fruiting bodies. Under favorable conditions, growth can go on indefinitely. One kind of mycelium growing in the humus of a pasture will grow in all directions in the form of a spreading disc. Eventually the nutrient in the inner portion of the disc becomes exhausted, and that part of

the mycelium dies, so that the living portion becomes a ring. Periodically, nutritional and environmental conditions are favorable to the production of fruiting bodies, and mushrooms then shoot up in a circle sometimes called a "fairy ring." Estimates based on measurements of the rate of growth of such rings have placed the age of some at three or four hundred years.

The metabolism of the fungi is plant-like in its independence of complex nitrogenous substances, but animal-like in its inability to get along without an external supply of sugar or other complex source of carbon. We might compare the metabolism of such a fungus to that of a typical green plant at night. Fungi, however, do not produce starch as their reserve food material as typical plants do; instead, they produce oils or glycogen. Some fungi also have the power of producing certain highly poisonous alkaloids, such as ergotin and muscarin. Since they are unable to manufacture their basic carbohydrate food elements, they have evolved the ability to secrete a great variety of enzymes through their hyphae, thus digesting the more complex organic compounds which they encounter. These enzymes or ferments include most of those generally found in green plants, but in most plants these enzymes are generally reserved for internal use, whereas the fungi use them extracellularly to digest the food upon which they grow. While some fungi

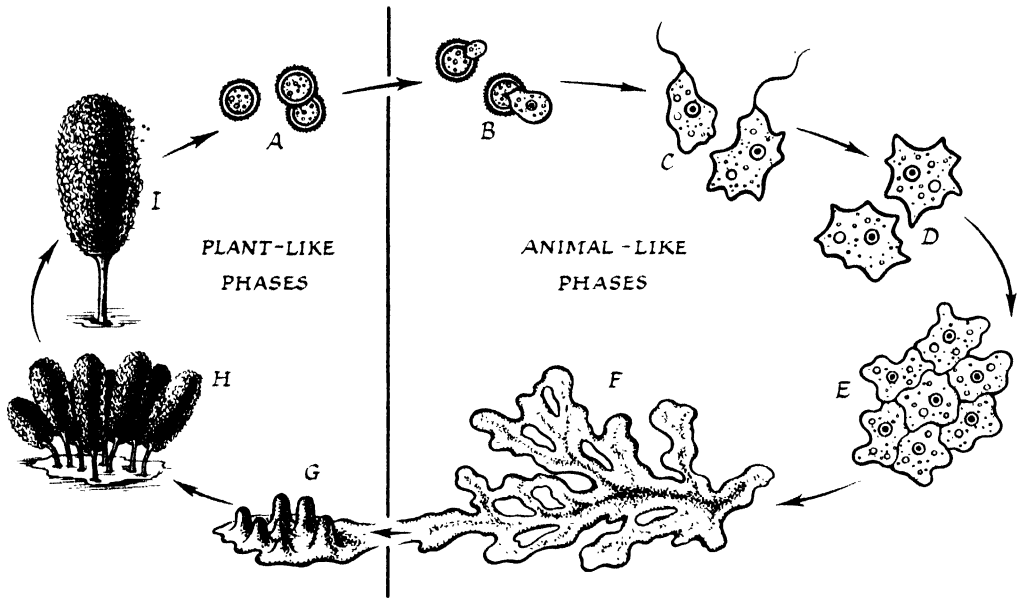


Fig. 191. Moments in the life of a slime mold. *A*. Spores. *B*. Spores germinating. *C*. Flagellated and partially amoeboid forms — single-cell phase. *D*. Some amoeboid single-celled phases. *E* and *F*. Small and large plasmodia. *G*. Beginning of sporangium. *H*. Mature sporangia. *I*. Single sporangium, enlarged.

are sharply limited in the variety of foods which they can utilize, others, such as *Penicillium* and *Aspergillus*, have an almost universal digestive ability and may grow on almost any organic substance. In the ability of the fungi to digest almost any organic compound lie both their usefulness and their threat to man. Thus they play a role parallel to that of the bacteria in the food cycles. But also like bacteria, they can attack and digest any form of organic matter, including many of our choice possessions. They may also attack us directly, as ring-worm does; or they may attack the plants on which we depend for food, clothing, shelter, and enjoyment. Most plant diseases are caused by various forms of fungi, and man's struggle against them costs millions of dollars annually. Though as direct foes they can hardly the bacteria, the fungi are among our most serious competitors. Fungi are largely parasitic, and thus in many cases considerably simplified in structure. They do not serve as a link with higher organisms, but are a group, albeit an important one, which occupies a niche all its own.

The Slime Molds

The Fungi are of four main types, the simplest of which are the slime molds, class *Myxomycetes* (Gr. *myxa* = mucus, slime). Of strange beauty rarely seen by human eyes, because of their growth in scattered forest spots and other out of the way places, these organisms are of uncertain classification, being completely unorthodox in form and structure. Sometimes they are unicellular, sometimes syncytial.¹ During certain phases of their life they display typical animal organization, sometimes like the protozoan amoebas and sometimes like flagellates, which are in their turn of uncertain classification. In other phases their behavior and structure is typically fungoid and hence plant-like. During the animal phase they are typical unicellular organisms, but in the plant phase they show strong trends toward multicellular organization. Could any organism be more difficult to pigeon-hole?

Economically and ecologically of no great

¹ Their colonial organization has been discussed on pages 160-161.

importance except for some types which cause plant diseases, the slime molds may be found underneath rotting logs or other vegetable matter, forming glistening masses more or less the consistency of raw egg-white. Some of these masses are very colorful, and with their fruiting bodies present a picture of great beauty. A single organized unit may attain the surprising size of almost a foot in diameter. An example is *Fuligo varians*, which may produce plasmodial masses like yellow cream on the surface of tanning solutions.

Life History. The sporangia of the slime molds grow on rotting logs and may range in size from tiny spheres to large flat masses a foot in diameter. Some are cylindrical, bearing a delicate network of fibers in which the spores are held until ready for release (Fig. 131). The spores are extremely small spherical cells which will germinate if they fall on a suitable organic medium and, if conditions are favorable, will soon be transformed into flagellated zoospores. After swimming about, and after repeated cell divisions, the flagellum is reabsorbed, leaving an amoeboid cell which now begins to crawl about on its substrate, ingesting organic matter as it does so. Soon members of cells of the same kind meet, at first forming small groups, then larger and larger ones, until they finally merge into large bodies containing many separate nuclei. Such a body is called a plasmodium. This behaves as a single organism, crawling about on its substrate like a giant amoeba, feeding, digesting, developing a dominant head-end, and egesting its wastes. For a piece of such raw and relatively undifferentiated protoplasm, it shows remarkable responsiveness to stimuli such as light and moisture, negative to the former and positive to the latter. Its most astonishing feat is the formation of the sporangia with which we began. Here the plasmodium achieves something completely beyond the capacity of an individual cell — something that can be achieved only by the collective effort of the individuals through a complete sacrifice of individuality. The sporangia are formed from the surface layer of the plasmodium, which hardens into

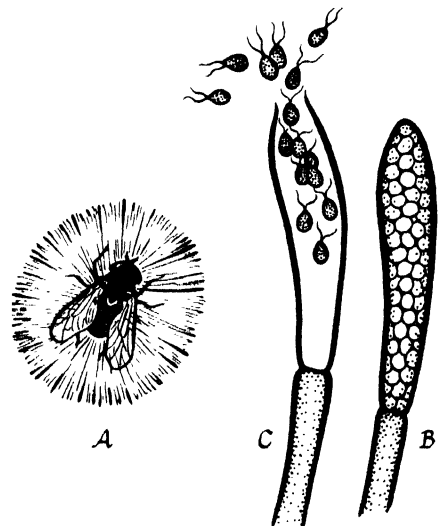
a wall. Nuclei which line the wall become separated from each other by secondary walls, forming the spores. These are supported by a mass of thread-like cells. Nuclear conditions indicate that a sexual phase takes place during the formation of the sporangium. Nuclei in the young sporangium unite in pairs, and those which fail to do so degenerate. Shortly before the separation of the spore nuclei by walls, meiotic cell divisions reduce these diploid zygotic nuclei to the haploid condition, which prevails through most of the life history.

These primitive processes suggest that slime molds may represent a very early phase in the evolution of multicellular life. Their flagellated phase further strengthens the assumption that flagellates may represent the archetype of multicellular organization.

Other Common Molds

The class *Phycomycetes* (*Gr. phycos* = seaweed + *mykes* = mold), named because of their similarity to certain green algae, includes numerous molds frequently found on particles of moist foods exposed to the air. In this group are the black bread mold, *Rhizopus nigricans*;

Fig. 132. Events in the life-history of the water mold *Saprolegnia*. A. An infected fly, with hyphae of fungus radiating from its body. B. Tip of a radiating fungus thread, early stage of sporangium formation. C. Sporangium discharging zoospores.



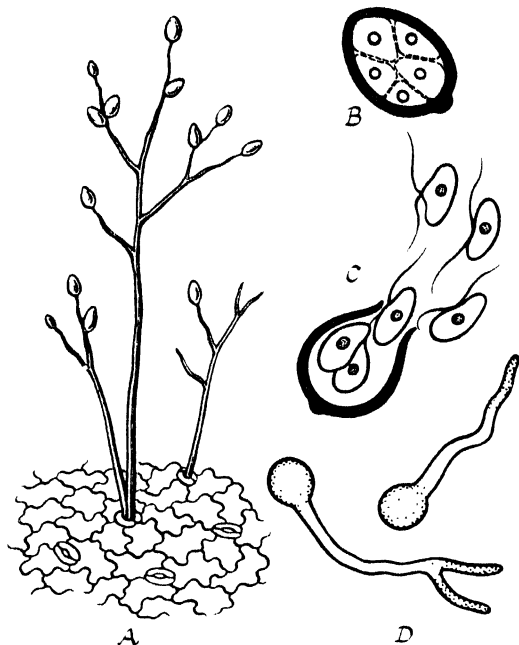


Fig. 133. Phases in the life of *Phytophthora infestans*, cause of potato rot. A. Potato leaf with sporangium-bearing filaments growing out of stomata. B. Ripe sporangium. C. Sporangium releasing zoospores. D. Zoospores producing new mycelium.

the white mold, *Saprolegnia*, which produces the cottony halos frequently found around dead insects floating in water; and *Mucor mucedo*, the white mold found on bread and fruit juices. Certain frequently parasitic forms, the mildews, are also of this class.

Characteristic is a plant body formed of slender tubular threads. These threads contain numerous nuclei but no cross walls, and so are basically similar to those of *Vaucheria*, the "green felt" of hot houses. Reproduction is both sexual and asexual. The latter occurs by means of spores, usually produced in sporangia partitioned off from the hyphae. In aquatic forms the spores are motile zoospores equipped with flagella. In terrestrial forms the spores are non-motile and floated away by air. Sexual reproduction, in the simpler forms, closely resembles that in certain algae. Each tubular antheridium grows until it touches an oogonium, whereupon it discharges its contents, including numerous nuclei, into the latter. In other varieties reproductive cells not differ-

entiated in form but produced in different individuals meet and fuse, so that their entire multinuclear contents mingle to form a thick-walled *zygospore*,¹ which may grow into a new mycelium.

Thus among the fungi there are sequences of evolution in reproductive mechanisms similar to those in the algae. *Saprolegnia*, the water mold (Fig. 132), found on dead organic matter and also infesting living fishes, is largely aquatic yet has abandoned the use of motile gametes, whereas closely related forms have not. In its sexual phase, *Saprolegnia* grows long tubular filaments with antheridia at their ends. These end in branched tubes which penetrate the oogonium and establish continuous protoplasmic paths for the sperm nuclei. Thus in its sexual phase the mold is prepared for terrestrial life. It is possible that this adaptation may have come about through selection as a result of exposure to atmospheric conditions while the mold was growing on floating or stranded matter. In the asexual phase, however, reproduction is by flagellated zoospores and is thus typically aquatic.

In *Phytophthora infestans*, a typical parasitic plant fungus and the organism which causes potato rot, spores falling on the leaf of the potato plant germinate and produce long hyphae which penetrate the leaf. Within the leaf, each hypha produces short feeding tubes, or *haustoria*, which pierce the leaf cells, absorb their contents, and thus destroy them. No part of the potato plant is spared from the advance of the despoiling mycelium, and if the plant succeeds in producing tubers, these will carry the infestation into the next growing season. Reproduction of the mold is asex-

¹ This is a very durable spore and tides the organism over poor conditions. When conditions are favorable, the zygospore produces a diploid mycelium. Spores produced in the sporangia of this diploid mycelium are produced by meiosis and are hence haploid. Haploid spores develop into a haploid mycelium. Thus the diploid mycelium is the sporophyte, the haploid, conjugating mycelium, the gametophyte. Since the latter can produce spores, the alternation of generations is not regular.

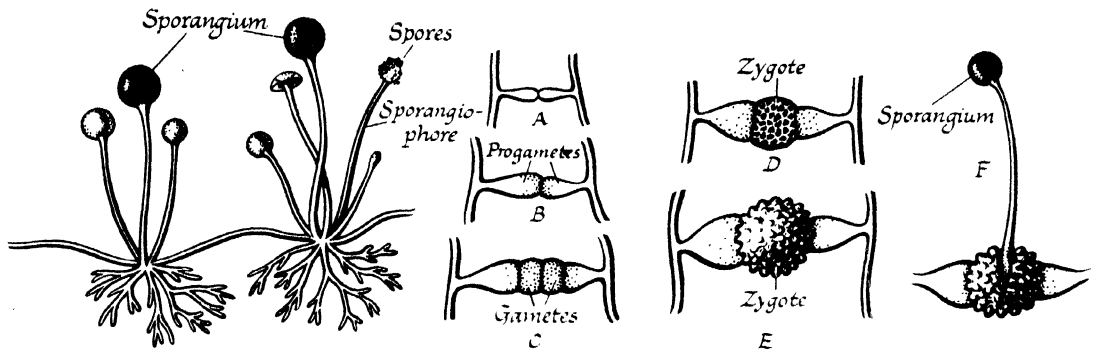


Fig. 134. Bread mold, *Rhizopus nigricans*. (After Mavor from Smith *et al.*) A–C. Fusion of gametes from different mycelia. D–E. Zygote formation. F. Germinating zygote.

ual by special hyphae sent out through the breathing pores, the *stomata*, of the leaf (Fig. 133). Again it is interesting to note that the spores produced on the sporangia of these special hyphae may either be carried away, like fine dust particles by the wind, or, if the leaf is moist, may still become flagellated zoospores suggestive of their ancestry. Similar mildews destroy the tissue of many plants.

Finally, *Rhizopus nigricans*, a common bread mold, displays peculiar reproductive features, though structurally it is similar to other molds already discussed (Fig. 134). Asexual reproduction is by spherical sporangia which grow on the ends of upright hyphae. Sexual reproduction occurs by the conjugation of multinuclear reproductive cells, which in turn produce multinuclear diploid zygotes. In *Rhizopus* as in other members of the group, conjugation is not indiscriminate but takes place only between certain mating types of individuals which are not obviously differentiated sexually but display some difference in vigor and are thus designated plus and minus.¹

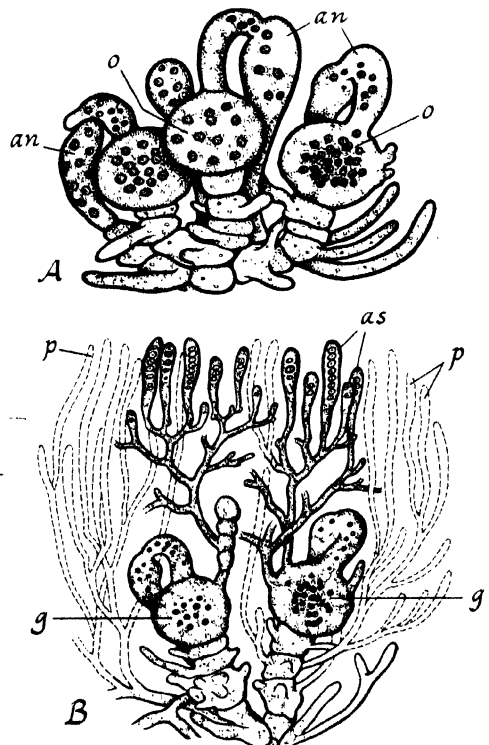
Yeasts and Related Forms

A third group, the sac or cup fungi, class *Ascomycetes* (Gr. *askos* = bladder), displays an exceptional range of form. Here are the yeasts,

¹ The terms plus and minus are used here because the two types display none of the most characteristic differences between male and female. And in *Mucor*, another bread mold, there are many such mating types, instead of only two, a multiplicity of sexes which we may well be glad to be free of.

the ergot disease of rye, the blue-green molds, the now-famous *Penicillium*, the fairy-like red-lined cup fungi, the edible morel, and the famous truffles. These are called sac fungi because at one phase of their reproductive cycle they produce spores within sac-like struc-

Fig. 135. Sexual reproduction in cup fungus, *Pyrenoma*. A. Female gametangia (*o*) shown in various stages of fusion with male gametangia (*an*). B. Gametospores (*g*) germinating and forming branching hyphae-bearing asci (*as*). Paraphyses (*p*) arising from the mycelium help to form the cup.



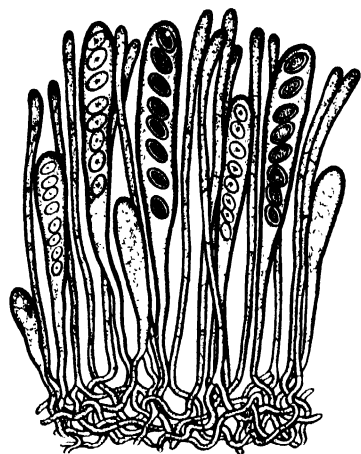


Fig. 136. Left: Ascocarps of cup fungi (*Pezizales*). Right: Formation of spores in cup fungi (*Peziza*).

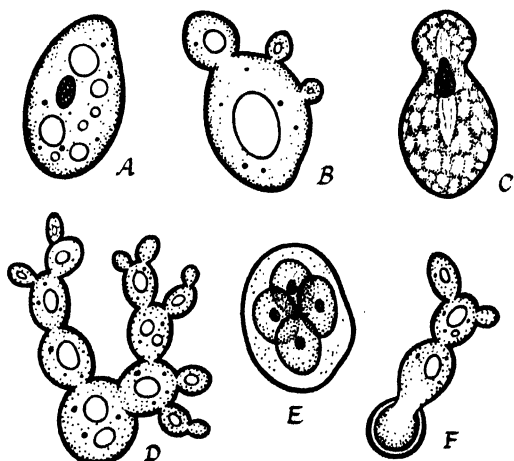
tures, or *asci*; these spores are consequently called *ascospores*. The plant body, the mycelium, has the same general structure as that of the previously discussed fungi except that the hyphae are not only divided by partitioning walls, but each compartment has a number of nuclei. Asexual reproduction is by upright hyphae which produce terminal spores, termed *conidia*, which are like rows of beads. Frequently, depending on environmental conditions, this phase alternates with a sexual one, in which special types of hyphae become intertwined, and fertilization occurs. In some forms, where distinctive antheridia and oögonia are produced, the resulting zygote germinates into a number of sacs, the asci (Fig. 135). Other less differentiated hyphae may grow up about the asci, sometimes producing large, conspicuous fruiting bodies (Fig. 136) which protect the asci. The various phases of this reproductive cycle are considerably modified in different varieties.

The yeasts, *Saccharomycetes*, show an unusual degree of degeneration or simplification. The plants rarely produce a mycelium (Fig. 137). The cells, frequently single but sometimes forming clusters or chains, are ovoid and reproduce by budding much like the formation of conidia. Under adverse conditions, a whole yeast cell may become transformed into an ascus, producing four ascospores within it. The formation of the ascus is preceded by the con-

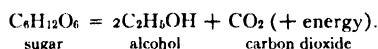
jugation of two cells; and meiosis then occurs in the formation of the ascospores.

Yeasts and Fermentation. Yeasts are of economic value since they cause fermentation, a process that results in the decomposition of organic matter, as in the production of alcohol. While other types of molds and certain bacteria also produce fermentation, such as the souring of milk or the ripening of cheese, yeasts are the main agents in the type which results in the transformation of sugar into alcohol, the be-

Fig. 137. The yeast plant, *Saccharomyces*. A. Single plant. B. Plant with three buds. C. Section, plant in cell division. D. Chain of plants produced by rapid budding and growth. E. Ascospores. F. Germination of ascospore and formation of new plants by budding. (After Wagner)

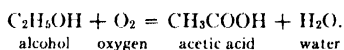


ginning and end products of which may be indicated as follows:



This process occurs in the absence of free oxygen and is termed *anaerobic* (living without air). Yeasts are able to carry on anaerobic respiration in the absence of free oxygen, although when it is present they engage in *aerobic* (living in air) respiration like that of most animals and plants. The anaerobic process is not an efficient source of energy, since only about 9 per cent of the available energy in sugar can be released by alcoholic fermentation. It is remarkable that the yeast plant can live and reproduce at all in the absence of oxygen. Since the spores of yeasts are found everywhere, it is almost impossible to keep fresh fruit or any exposed liquid containing sugar for any length of time without fermentation, and even bottled sweet liquids must be sterilized if they are to keep.

Although wines and fermented beverages are produced spontaneously by yeasts, other fermentation processes may interfere, causing different results. Thus in the presence of oxygen, acetic acid bacteria may cause the following reaction:



The product, acetic acid, may cause wine to become vinegar if it is unduly shaken or exposed to the air during fermentation.

Since CO_2 is produced in alcoholic fermentation, yeast has become of great importance in the leavening of bread. The tiny bubbles of carbon dioxide separate the dough into thin layers, thus producing its fine texture, since yeast continues to multiply in the dough until killed by heat. Masses of dough left from a previous baking may be used to leaven a new batch. This was once the universal method, though today yeast is commercially cultured and sold. It is of course possible to use other methods of introducing bubbles into dough. Any substance that produces a non-noxious gas without leaving an undesirable residue will

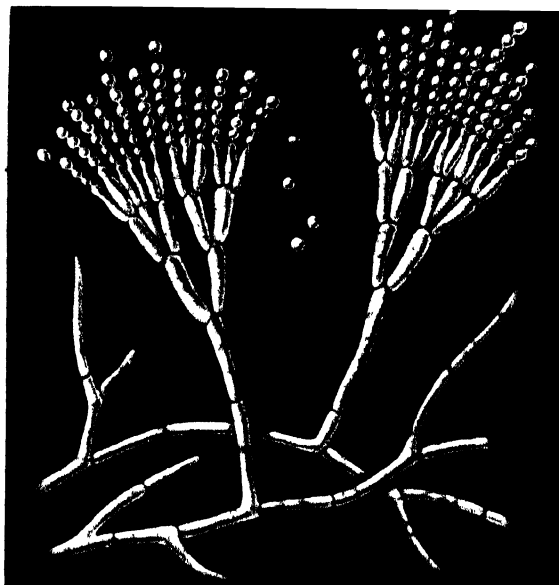


Fig. 138. *Penicillium*, structure and spore formation.

serve the purpose. This is the principle of baking powder.

Penicillium. This blue-green sac fungus has soared to sudden fame in the past few years. Although it is one of the commonest and most widespread of molds, its ability to produce substances which inhibit the growth of bacteria was not discovered until recently. The now famous variety is *Penicillium notatum*. Less publicized but long known and highly appreciated are *Penicillium roqueforti* and *Penicillium camemberti*, which are responsible for the special flavors of two fine cheeses. Although the anti-bacterial properties of *Penicillium notatum* were described by Alexander Fleming in 1929, no use was made of them until over ten years later, because of the difficulty of producing penicillin in large quantities. The war, and the consequent need for anti-bacterial agents, rocketed penicillin to fame. It is an extremely potent and relatively non-toxic agent in the treatment of various infectious diseases. Solutions as weak as one part in a hundred million are effective in stopping the growth of such organisms as *Staphylococcus*, the organism active in certain types of infections.

Other Forms. Several other members of this class are worth brief mention. Powdery mildews frequently produce a white bloom on leaves of a wide variety of plants. Some are

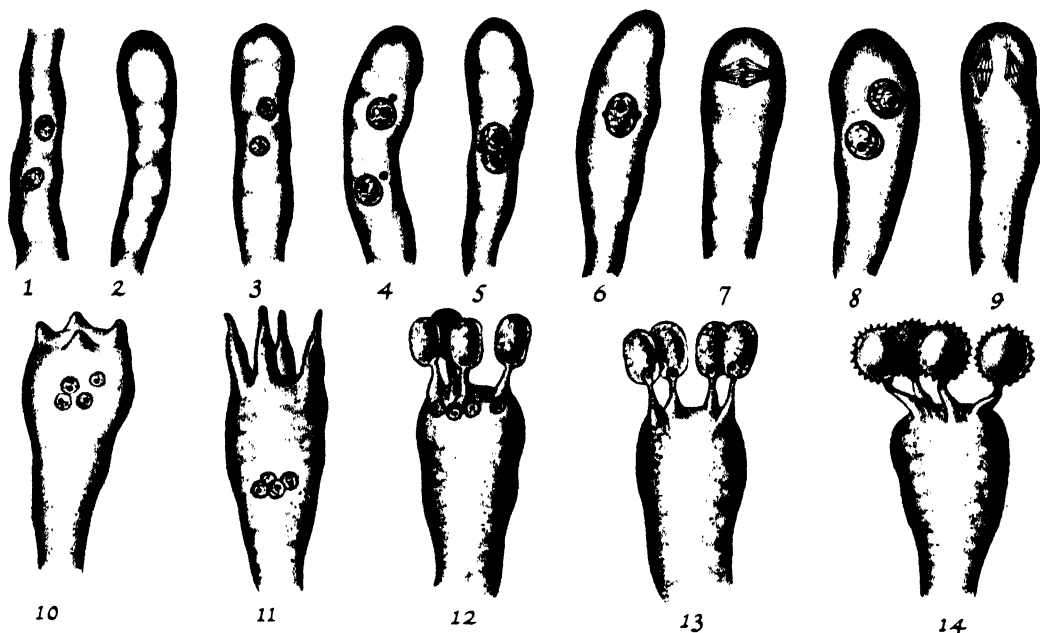


Fig. 139. Basidia and spore development. 1. Portion of a hypha with two nuclei. 2. Young basidium without nuclei. 3. Young basidium with two nuclei probably from hypha. 4. Slightly older stage. 5. The two nuclei beginning to fuse. 6. Basidium with nuclear fusion completed. 7. Fusion nucleus dividing. 8. After first division. 9. Daughter nuclei dividing. 10. Basidium with four nuclei. 11. Later stage. 12. Young spores forming. 13. Nuclei entering spores. 14. Mature spores with formed walls.

relatively harmless, whereas others may seriously damage the plants. *Claviceps purpurea* is responsible for the disease known as ergot on rye and other grasses. Highly poisonous substances, formed by this fungus, have been found to be useful in medicine. The substance *ergot* arrests hemorrhage, may hasten labor in childbirth, and is useful for other purposes. The edible morel (Fig. 129) and the truffle present an odd contradiction to most of the sac fungi, in that they are not only edible — so is yeast — but are even considered delicacies.

Under suitable conditions, yeasts grow with phenomenal speed, producing valuable proteins from simple nitrogenous compounds. For these reasons they hold great promise as a valuable food source in a hungry world. Varieties of yeasts have been produced which are said to simulate meats in flavor and nutritive value. Thus it may soon be practicable to use cheap surplus molasses and other by-products to produce nourishing and palatable food.

Basidiomycetes

A final group of fungi is the class *Basidiomycetes* (Gr. *basis* = base), which derive their name from the fact that their haploid spores are produced by meiosis on diploid club-shaped spore mother-cells called *basidia* (Fig. 139). This group includes not only all the common mushrooms and toadstools, but also certain viciously destructive plant parasites known as rusts and smuts. The basidia often become overgrown by complex protective structures and are produced on complex, more or less woody mycelia, as in the mushrooms and toadstools. The mycelium is segmented, as in the sac fungi, and in the higher Basidiomycetes, it is diploid.

Rusts. Among these fungi is *Puccinia graminis*, cause of the black stem rust of wheat and other cereals, and because of the immense damage it causes (the 1935 epidemic caused losses of \$100,000,000 in North Dakota alone), it demands our attention. The life cycle is

greatly complicated by the peculiar habit of alternating between two unrelated hosts, the European barberry and the wheat plant or some other grass. Black winter spores (*teliospores*) dormant on the stubble of infected wheat plants all winter, germinate to produce another type of spores (*basidiospores*) which now infect young barberry leaves. Here, after a complex sexual cycle, involving male and female (or better) plus and minus filaments, binucleate *aeciospores* are produced which must be carried by wind to wheat plants. The mycelia which form here eventually produce patches of rusty brown summer spores (*uredospores*) which may spread the infection to other wheat plants. Later teliospores are again produced, thus closing the cycle.

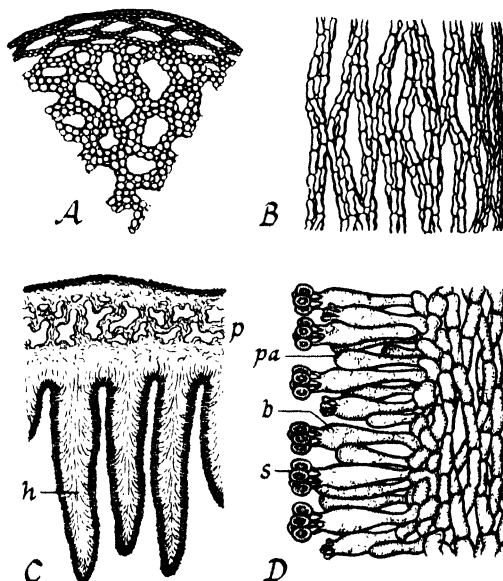
It is evident that the disease could be eradicated by breaking the cycle, and the most obvious method would be to eradicate the intermediate host, the European barberry. Laws have been passed in this and in other countries to this effect, and where thoroughly carried out, have proved effective. But this is not easy. Barberry plants are prolific and may easily be overlooked. It was found, in one case, that a small hedge of barberries, planted near a house, in thirty years produced 35,000 bushes spread over an area of 300 acres, disseminated by cattle and birds. When it is considered that wheat as much as a mile from a barberry plant may become infected, and that a single leaf of a barberry plant may produce 8,000,000 or more spores, the difficulty of the task may be appreciated.

Because of these difficulties, plant breeders have attempted to produce resistant strains of wheat, with some measure of success. But these attempts have brought to light some astonishing facts. *Puccinia graminis* is not restricted to one kind of wheat only, nor even to wheat. That is, it has several strains which can live on various host plants. At least six forms have been found, some specializing on wheat, some on rye, others on oats or various other grasses. But that is not all, for each of these forms is in turn divided into many minor races according to their ability to attack vari-

ous strains of wheat. In the type which attacks wheat, no less than 70 forms have been determined, and it is estimated that there may be as many as 1000 different biological strains all told, each with its own specific heritable characteristics. It is remarkable that this variability in the choice of host plants does not extend to the barberry phase. This may be explained by the wide choice of closely related grasses, artificially sponsored by the work of plant breeders, as compared to the neglected barberry. Attempts to produce rust-resistant cereals are a constant race between the achievements of the plant breeder and the emergence of further mutant races among the prolific rusts under the guidance of the adaptive factor of selection.

Smuts. These pests are painfully familiar to almost every backyard gardener as black, puffy masses filled with a sticky slime, which grow on corn and other plants. The sexual phase is limited to nuclear fusion previous to spore production. Spores, falling upon the seeds of the

Fig. 140. Mushroom structure. *A* and *B*. Cross and longitudinal sections through stem showing arrangement of hyphae. *C*. Tangential view of the gills — *p*, pileus; *h*, hymenium, appearing as a dark band on gill surface. *D*. Portion of the hymenium enlarged — *b*, basidium; *pa*, paraphysis; *s*, basidiospore. (After Curtis)



host, germinate and produce a mycelium which adjusts its rate of growth to that of the young host plant. As the host matures, the fungus also matures and produces vast masses of black spores which scatter and infect new seeds for a new crop the following year.

Mushrooms and Toadstools. The most familiar of the fungi is the order *Agaricales*, which includes the mushrooms and toadstools (Fig. 130). Most of these plants are relatively harmless to other living organisms, since they generally grow on dead organic matter, on the humus in the soil, on animal refuse, or on rotting wood. A few, however, are poisonous when eaten, and some attack living trees. The body of the plant is the hidden mycelium, and the visible toadstool or mushroom is only the reproductive structure. A ball-shaped top becomes transformed into a cap, which bears numerous gills on its under side. The gills are masses of hyphae (Fig. 140), at the ends of which are produced basidia, and eventually upon these the quartets of tiny haploid basidiospores. These are scattered by the wind, or by insects, and where they drop they produce new mycelia if conditions are favorable. There are numerous variations of sporebearing tissue.

The bracket fungus, frequently seen growing on trees as a woody, shelf-like structure, grows numerous fine pores on its undersurface instead of gills. These are lined with basidia. In the puff-balls, some of which look like over-sized eggs dropped on a lawn, the interior cavity is filled with a sponge-like network of smaller cavities within which the basidia form their

spores. When the puff-ball matures, the inner spongy material breaks down, leaving the outer tough skin filled with countless millions of spores. The puff-balls are considered the most prolific living things on earth. It has been estimated that a puff-ball about a foot in diameter — and these are not the largest — may produce as many as seven trillion spores, each capable of producing another puff-ball just like itself. Seven million millions of reproductive cells from one individual at once — or over three thousand times as many as there are people on earth!

Summary

In the algae we have traced the development of cellular differentiation from extremely simple unicellular organisms so undifferentiated that they have plant and animal characteristics in almost equal balance, to highly developed plants with the basic structures, such as root-like processes and short leaves, necessary for survival on land. We have also seen how the algae reflect the gradual development of sexual reproduction and the alternation of generations found among all higher plants. The fungi, without chlorophyll and all either saprophytic or parasitic, are divergent from the main line of development in the plant kingdom. Our brief glance at the algae and the fungi has enabled us to trace some of the evolutionary processes that lead to the higher plants, and some of the ways in which these organisms are important to other living things, including man.

Plants Invade the Land: Mosses and Ferns

THE PROBLEM

Plants before the Landward Migration

Modern knowledge leaves no doubt that land plants descended from water plants. The question is, How? For no belated adaptation to land life could have benefited a plant after it had been washed ashore unless it had previously possessed adaptations making shore life possible.

It will be recalled that a preliminary feature which contributed greatly to successful survival on land was the loss of mobility that came with the alternation of generations. This made possible a conservation of energy which greatly increased the chance of survival of large plants, both in the water and on land: indeed, mobility on land would have posed almost insuperable difficulties for plants at the outset. Second, the transition from a single-celled to the multicellular condition not only had resulted in larger, tougher plants, but the specialization made possible by multicellular organization had produced root-like organs, stem-like structures for transporting substances within the plant, heavier, sturdier cell walls, and leaf-like structures. The advantages of sexual reproduction were retained, though the gametes were still motile and on land could meet and unite only under periodically favorable conditions of moisture which lasted long enough for the gametes to perform their function. In its immobile vegetative phase, the plant could then survive conditions that would have spelled extinction to the less successfully adapted gametes. Sexual differentiation also contributed toward preparation for land life in another way, for larger eggs permitted larger embryos that could more quickly establish themselves

under difficult conditions. Thus the thallophytes were prepared for land life before the landward movement began.

Obstacles to Life of Plants on Land

Living conditions in the water are uniform and simple, and the raw materials needed by the plant cell for its metabolism surround it on all sides. Water, containing dissolved salts and carbon dioxide, bathes all its membranes, and sunlight filters through the water. Thus the chlorophyll-bearing organism has all it needs for a survival. If the plant cell is a floating one, a simple cell wall is quite sufficient to protect it against mechanical injury, and thus even the simplest microscopic cell has a fairly good chance of surviving. But the situation on land is quite different. Sunlight is more abundant, but the air will dry out an unprotected plant cell in a matter of seconds. And water, with its necessary salts and carbon dioxide, is usually present only in the soil, where there is no sunlight. Thus the plant's two main needs are supplied from different directions, and consequently in order to survive in such an environment it requires a certain degree of specialization, a root which can project into the earth to absorb water, and a shoot above ground for photosynthesis. In its simplest form this division consists of a few absorbing threads at the base of a leaf-like thallus, as in *Marchantia*. Moreover, the shoot must be protected from desiccation, but not by an impervious cell wall, for this would interfere with the gas exchange necessary for photosynthesis. The situation is clearly a difficult one, and it is evident that an organism capable of surmounting the obstacles it sets up must indeed be delicately adapted.



Fig. 141. Mosses: left, specialists in frugality, they grow on bare rocks; right: sporophytes growing on the gametophytes.

The Necessary Adaptations

Root and Shoot. In order to survive under true land conditions, then, a considerable degree of specialization is necessary, and five main developments must have taken place. The first of these, as we have already seen, is *the division into root and shoot*, the root in simplest form consisting of a few hair-like threads attached to a thallus.

Vascularization and Fibrous Structures. The second and third of these developments seem to have gone hand in hand. These were the appearance of better means for the transportation of substances within the plant by means of tubes and ducts, that is, vascularization; and the addition of fibrous structures to give increased strength to the stem or trunk. It appears that competition between plants soon demanded that if a species was to survive it must either lift its photosynthetic surface high enough toward the light or else so change as to survive with what little light other, taller plants might let through. As we might expect, both possibilities came to pass. For those plants that could not survive without ample light, extinction could be avoided only by the development of stems and trunks. And again both things occurred. The evolution of a stem

resulted in further separation of the two essential working portions of the plant, the photosynthesizing parts and the absorbing and anchoring roots. Since substances had to be transported between these two regions, the emergence of a vascular system, a system of tubes and ducts, had great selective value. Through such vessels sugar solutions manufactured in the leaves could be transported to the dependent roots which then could build their protoplasmic compounds, while life-giving water with its freight of dissolved salts could in turn be transported from the roots to the shoot and the leaves. So lengthened, a trunk would require fibrous structures strong enough to bear the weight of the upper portions of the plant. We have not forgotten, of course, that need never guarantees or in any way induces the appearance of a fulfilling structure; the environmental stencil has simply been set to capture the rudiment of such a structure at once, by selection, should random mutations produce it.

The environment demanded two further basic modifications if the organism was to survive successfully on land. These were a special organ of photosynthesis and further modifications in the reproductive system.

Leaves. The first of these, the leaf, was probably the more immediately important. Survival in the environment demanded an organ of sufficient size that would combine permeability with special provisions against water loss. Again, among the innumerable mutations that have appeared since life began, there came those which made such a structure possible, and the selective environment assured their perpetuation.

The leaves of aquatic plants perform a relatively simple function. But the function of the leaves of land plants is considerably more complex, and the demands placed upon them are conflicting. In order to absorb light for its primary task of photosynthesis, a leaf should present a large cell surface. The larger the plant, the greater, relatively, should its leaf surface be, for volume grows proportionally to the cube of the dimensional increase, while surface grows in proportion only to the square. In other words, the leaf area must increase more rapidly than the plant as a whole. In succeeding chapters, particularly in Chapter 12, where the vegetative structures of plants are discussed in some detail, we shall discover various devices which achieve this increase in surface.

The successful functioning of the leaf further demands cells with a relatively free access to air, especially to carbon dioxide, which is vital to its work. That is, a green surface capable of photosynthesis must be porous. Yet since this permeability must not result in too much loss of water, the leaf must possess an unusual combination of traits to prevent desiccation, or drying, without asphyxiation. Were we to seek by reason a way of reconciling these conflicting demands, we should probably arrive at devices similar to those which were finally evolved by plants through random mutations and natural selection. A plant might be made to meet the situation by a leaf surface which could be reduced whenever a shortage of water threatened, and this could be done in several ways. One of the simplest would be to have the leaf curl up into a tight roll. Another would be to house the delicate-walled photo-

synthetic cells within a shell of coarser thick-walled cells. Portals through this housing could provide ventilation, and could be closed in times of water shortage. Such photosynthetic organs are not the mere creation of our imaginations; we have given the very description of the kinds of leaves that evolution has actually produced in modern plants. The rolling up of the leaves, obviously a simple adaptation, is found in certain mosses. Most higher plants are equipped with waterproof leaves studded with openings that may be closed by valves. In general, the demands of the environment selected, in time and by degrees, a structure that consisted of freely permeable photosynthesizing cells which could be almost completely shut off from the air by impervious cells if the water loss became too great. How this was accomplished we shall see later in this book.

Reproduction. The fifth and last requirement imposed by the environment was a change in the processes of reproduction. Sperm cells that must swim outside the tissues of the parent plant are poor risks for survival on dry land. For this reason plants that did not evolve a substitute for this type of gamete remained always tied to life in moist places. Even when reproduction occurs by spores, the spores that are satisfactory in the water are not necessarily suitable on land. A new type with a tough protective membrane would have marked advantages, and we find that many of the plants which have survived have evolved them. On the other hand, if sexual reproduction with all its advantages were to be maintained, then the two nuclei from different cells must somehow be enabled to meet. If not by swimming, then they must fly — crawling never seems to have been introduced — or the parent organisms must be in contact, either directly or by some sort of bridge. Modifications of all these kinds were actually evolved. The first land plants, however, still reproduced by swimming sperm cells, and thus required considerable surface moisture. For this reason they are amphibious rather than actual dry-land plants.

Forces Behind the Landward Movement

In view of all these obstacles and requirements, and of the barren inhospitality of the land, we may wonder how plants ever came to live on land at all, especially since any structures essential to survival on land had to exist before the plant even ventured beyond the water. We may imagine such preparatory selection to have occurred in the tidal zone. Plants like the rockweed, alternately exposed to air and submerged at high tide, exist where they do by virtue of certain structures that may well be considered pre-adaptations to life on land. The rockweed has developed "holdfasts," which are a natural pre-adaptation for roots, regional differentiation of tissues into an epidermal layer resistant to moisture loss, and an inner region already equipped with vascular or conducting tissue, even to the production of clearly defined sieve tubes, so characteristic of higher plants. Thus such a plant survives long periods of exposure to the blazing sun, has rudimentary roots and the beginning of a vascular system to connect these with the rest of the thallus. It is pre-adapted for a possible future life on land.

In their representative systems, some aquatic plants had evolved a form of conjugation that did not depend on swimming sperm cells, for instance the green alga *Spirogyra*, the pond scum. These adaptations were not all combined in any one plant, however, and those in which they did occur were in other ways clearly not suited for land life. The fact that such adaptations are found in strictly aquatic plants strengthens the view that those adaptations which would make land life possible came about through fortuitous mutations. So we may assume that a plant that survived after it had been cast upon the shore did so through a chance combination of developments which were advantageous, or at least not disadvantageous, to survival in the water.

But another question arises. Granted that a plant capable of life in the tidal zone develops, why should it live in that region rather than in deeper water? Here we must consider that

the long span of evolution that had developed aquatic plants and animals had produced large numbers of highly efficient organisms. This is another way of saying that life in the water had undoubtedly reached a stage of exceedingly keen competition. Since the land above water was completely devoid of life, the first land plant was freed of this competition, and hence would have tended to survive if well enough adapted to the conditions presented by the inanimate world. This must be considered to have been an advantage of no mean order.

The First Land Plants

As we have seen, it is possible to reconstruct the minimum development of the first land plants which were able to survive. We may now turn to paleobotany for evidence of what the first known land plants actually were like. The pages of this record are incomplete, and the primitive land plants which have left some traces are not necessarily the first that existed. One of the earliest known ones, *Zosterophyllum*, was discovered in Australia and dates back to the Silurian, well over 350 million years ago. Then in the next age, the early Devonian, are found the three strikingly primitive plants *Rhynia*, *Hornea*, and *Asteroxylon*. As we might have expected, all three of these are divided into root and shoot (Fig. 142). *Rhynia* shows a primitive root which consisted only of tufts of hair-like processes scattered over the lower portion of the shoot or stem, which was underground. *Rhynia* and *Hornea* were both leafless, and in this way do not fully meet our expectations, but we are justified in assuming that they were green and that the shoot served the function of photosynthesis, for it was equipped with ventilating pores, called stomata, quite similar to those which we postulated for the leaves of land plants. Shoots of these plants were equipped with ducts, although sparsely. Thus with root-like structures, with ducts, and with breathing pores, the plants were clearly adapted for land life, although in a very primitive manner. So general are these plants in their features, and so unspecialized, that bot-

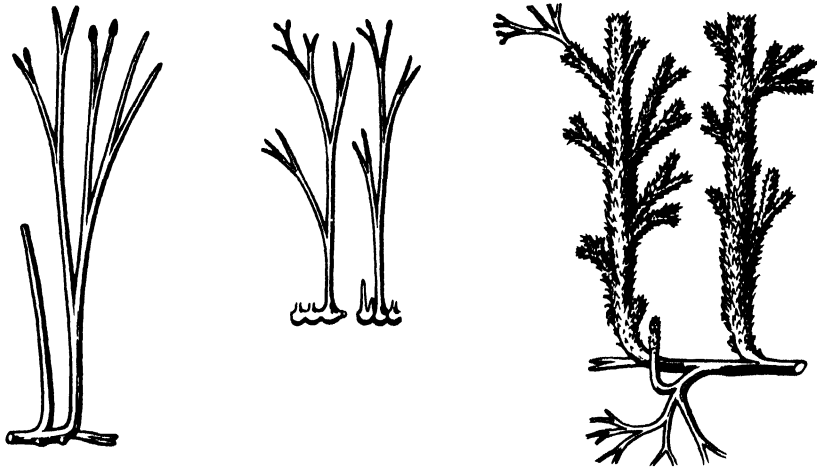


Fig. 142. Representatives of the first known land plants, *Rhynia*, *Hornea*, and *Asteroxylon*, appear to meet the minimum requirements for life on land: green shoots with breathing pores, rudimentary ducts, and tuft-like roots. Spores were produced at the tips of the branches.

anists find it difficult to agree whether to place them with the algae, the mosses, or the ferns.

The manner of reproduction of these earliest land plants also indicates their adaptation to land life, for the spores were heavily cutinized, that is, surrounded with heavy walls, which protected them against drying out. No fossil record of the sexual phase of their reproductive cycle has been found. But this is not surprising, since this phase of the plant was probably very small and delicate, as it is in modern primitive plants. The spores were produced in capsules or sporangia at the tips of the branched shoots, in a manner similar to that found in modern ferns.¹ In *Hornea* each sporangium had a sterile column extending up through its center, similar to the columella, to be noted shortly, in the sporangium of the moss. The whole form of *Rhynia*, with its lack of leaves and its simple stem-like body structure, suggests close relationship to the algae.

Two Modern Relatives

Asteroxylon had simple scale-like leaves which had no vascular connection with the stem and which gave the plant a rather prim-

itive aspect. This plant may be a forerunner of the lycopods or clubmosses, such as the ground pine, frequently used for Christmas decorations (Fig. 151). Two strangely isolated living plants which deserve mention because of their striking fossil affinities are *Psilotum* and *Tmesipteris*. These living fossils, so similar in appearance to the fossil *Rhynia*, show little resemblance to any other modern plants. Like the earliest plants, they are virtually leafless and still quite rootless, having an underground stem, or rhizome, which serves as a root, assisted by the mycelium of symbiotic fungi. Like those of *Rhynia*, their leaves are minute scales, and photosynthesis is performed largely by the green cortex of the stem.

DEVELOPMENTS IN REPRODUCTION

Evolution of the reproductive system of plants as they moved onto the land is an involved story. The first plants to emerge from the water still retained the ancient method of reproducing sexually by means of swimming sperm cells. Alternation of generations made it relatively simple for plants to achieve satisfactory dissemination by means of spores while still maintaining the advantages of sexual reproduction. Cutinization of spores represents

¹ See pages 201-202.

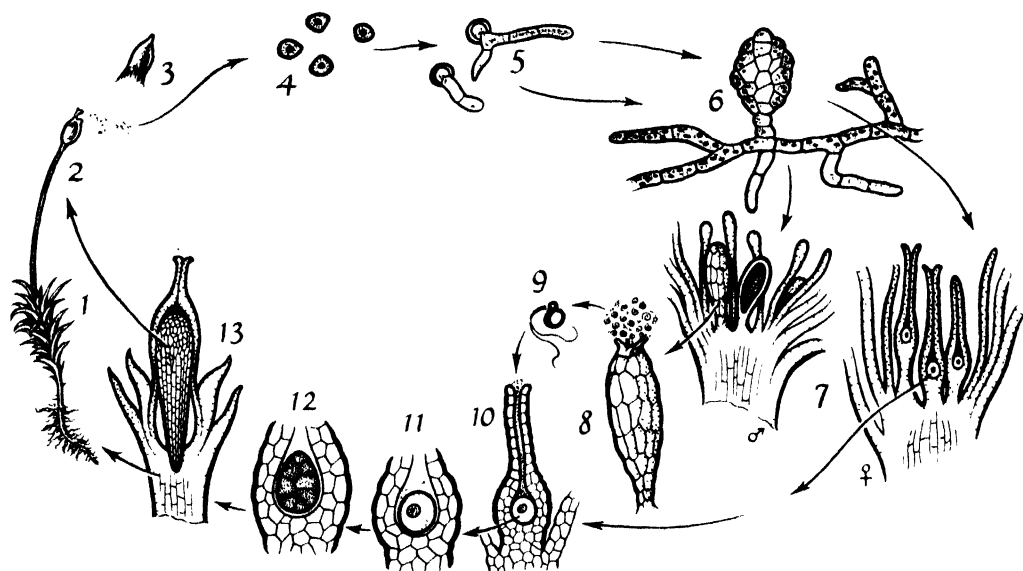


Fig. 143. Life cycle of a moss plant. 1. Mature female gametophyte, the moss plant, with ripe sporophyte, (2) growing upon it and discharging spores from its capsule. 3. The calyptra which previously covered the spore capsule. 4. Ripe spores. 5. Germinating spores. 6. Young gametophyte growing on thallus-like protonema. 7. Tips of male and female gametophytes, with antheridia and archegonia. 8. Antheridium discharging sperm. 9. Sperm cell, greatly magnified. 10. Archegonium with egg cell. 11. Zygote in archegonium. 12. First growth stages of sporophyte in archegonium. 13. Later growth of sporophyte.

the first obvious adaptation towards better survival of the units for dissemination on land, and indeed some Silurian plants which may be considered algae already had spores surrounded by a hard protective coating.

On land, the two phases of the plant reproductive cycle need quite different conditions. Spores are more effectively disseminated if they are released as high above the ground as possible, so that they may be carried a long distance before settling to earth again. It is also advantageous that they be dry. These conditions are met only if the sporophyte is tall. The gametophyte, however, must be where it can obtain enough surface moisture for the swimming sperms, and this is more likely to be found near the ground. This is indeed an exacting set of requirements.

The Mosses

In one of the most primitive of the amphibious plant groups of today, the mosses, we find apparent adaptations to such demands.

The gametophyte of the moss is the familiar moss plant itself, which always remains low-growing and thrives in moist, shady places. In the crown of the moss plant are the gamete-producing structures, the *antheridia*, for sperm cells, and the *archegonia*, for egg cells. The sperms, released from their container, swim through the film of moisture on the surface of the leaves and between the closely packed little plants, until they find an archegonium. They then swim down through its narrow channel to an egg, which they fertilize. The zygote thus produced grows by cell division and becomes an embryonic sporophyte while still within the archegonium (Fig. 143). Whereas the gametophyte moss plant is green — that is, performs its own photosynthesis — the young sporophyte grows as a virtual parasite upon it, since it is either colorless or only very slightly green. With the food materials supplied by the gametophyte, however, it grows into a long slender stalk on the top of which the spore case develops. Eventually

this bursts, releasing the now ripe spores which have been produced within it. Each spore, if it falls into a suitable environment, will give rise to a thallus-like structure called the *protonema*, and buds developing on this grow into a gametophyte, so completing the cycle.

Weaknesses. Let us examine the weaknesses and conflicting refinements in this reproductive cycle. The gametophyte, with its swimming sperm cells, requires low growth near ground moisture. But it also produces all the food for both generations, and to do this most efficiently, it should be tall so that it could absorb a maximum amount of sunlight in competition with neighboring plants that struggle to outgrow it. Here are two conflicting requirements, and between them only a compromise seems possible. The sporophyte should be tall for the most effective dissemination of the spores, but since it grows as a parasite on the gametophyte, its growth is necessarily limited by the capacity of the latter to produce an excess of organic food beyond its own needs. Furthermore, since the sporophyte is tall, it is in a favorable situation for photosynthesis; yet it fails to utilize this advantage. Thus there are conflicting demands on the sporophyte also. All in all, the moss plant appears to be a sorry compromise, and the wonder is that it has survived in competition with plants that have reached a much higher state of efficiency. Perhaps it has survived because, so to speak, it made a virtue of necessity. Crowded into odd corners generally unfavorable for plants, the mosses yet reproduce and survive on little light and poor and meager food. They have become specialists in frugality; they have survived even as the pushcart merchant survives in the shadow of the giant department store.

It is not difficult to suggest changes in the moss plant which would probably make it more successful. Most obvious of these is the abandonment of the antiquated and inefficient free-swimming sperm. Or the gametophyte might well be less of a compromise. Indeed, it would probably be most efficient if it were a simple thallus whose sole function was sexual reproduction. Then it could be really low

and so be nearer to the moisture which the sperms require. That would mean that the sporophyte would have to abandon its parasitic habit, which appears rather impractical anyway. Since it now grows as tall as it may, to disseminate its spores, it would be more efficient if this tallness were also utilized in the production of chlorophyll and the development of leaves. Through the independence thus gained, the emancipated sporophyte could grow still higher. Indeed, growing on its own roots and provided for by its own leaves, it could reach a height limited only by the extent of its other improvements, such as strengthened fibers and better ducts. Such increased height would give the plant a great advantage in competition for sunlight. These "proposals" for the moss plant, in fact, describe just what has happened in the evolution of the higher plants.

The Ferns

The plant which we have imagined corresponds in general to the ferns (Fig. 144). In these the spore develops into a miniature heart-shaped thallus which meets only the minimum requirements for an independent plant: a green thallus above the ground and a few colorless root-like hairs, called *rhizoids*, below. Eggs and sperms are produced in archegonia and antheridia, as in the mosses. The sperm cells swim through their film of moisture to the egg. The resulting zygote germinates and sends its own roots into the ground and its green shoot up into the air. The gametophyte, having performed its function, is now useless and is crushed out of existence by its much larger offspring, the fern plant itself. The fact that ferns may grow to the height of tall trees proves the advantage of their structure over that of the mosses in the matter of reaching the sunlight. And yet, despite all improvements, the definite handicap of the swimming sperm still persists in the group. The weakness in the fern cycle is unquestionably the miniature gametophyte, so extremely delicate and vulnerable, and the swimming sperm cells that it produces.

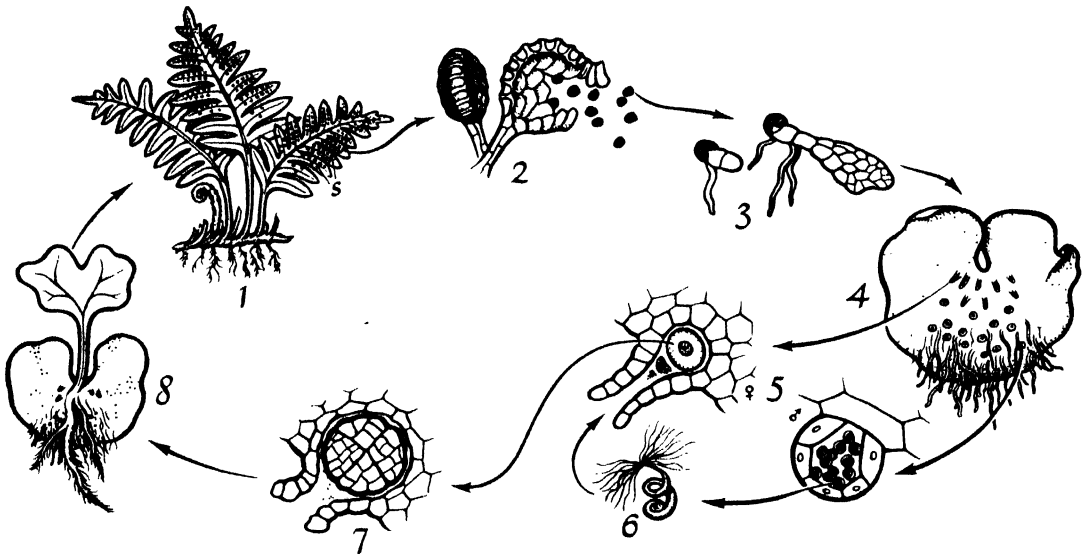


Fig. 144. Life cycle of a fern plant. 1. The sporophyte fern plant with clusters of spore capsules (s) on under sides of leaves. 2. Spore capsules. 3. Spores germinating by cell division to produce a prothallium. 4. A prothallium (the gametophyte). 5. Antheridium (♀) and archegonium (♂), growing on the prothallium. 6. Sperm cell. 7. Embryo sporophyte in archegonium. 8. Young sporophyte growing out of archegonium.

If we were to “improve” the fern, as we did the moss plant, we would wish to see the weak link in its cycle, the tiny gametophyte, either strengthened and enlarged or else protected. We should also wish to see the free-swimming sperm eliminated. We shall find that evolution in higher plants actually led to protection of the weak gametophyte rather than a strengthening of it, and we shall find that the swimming sperm too was eliminated, though very gradually. Briefly, let us see how this happened.

Although mosses are probably not direct ancestors of ferns, they may be used to represent a primitive beginning of land plant life. The most obvious change in the reproductive mechanism of the ferns, as compared with that of the mosses, is the reduction in size and relative importance of the gametophyte. It is this reduction in size that makes the gametophyte of the fern such a weak link in the reproductive cycle and so ties it to moist places, since it is so easily injured or destroyed. Despite this, we see a gradual further reduction in the size of the gametophyte as we trace the evolution of plants to higher and more modern forms. The minute size, and hence the vul-

nerability, of the gametophyte, is more than outweighed by the protective structures which have evolved around it. For in certain ferns, the gametophyte is retained *within the structure where it is produced*, a feature only possible because of its reduction in size. Thus, in *Selaginella*, the gametophyte develops within the spore capsule of the spore which produces it.

The First Seeds

In higher forms the spore is not even discharged from the sporangium, but remains within this relatively safe housing, there to undergo cell division and to become a gametophyte. The gametophyte may then even produce gametes, which become embryonic sporophytes, all still within the old sporangium of the preceding generation — a veritable Chinese box-within-a-box. Indeed, the old sporophyte may even take part in this process by growing further protective structures around the scene of activity, in the form of fruit and seed housings. The fossil pteridosperms, or seed ferns, were probably the first plants that evolved these stages in their mode of reproduction. In these earliest seed-plants, the spores were re-

tained on the leaves in the capsules where they were produced, and were thus enabled to grow into gametophytes which in turn produced gametes and a young generation of sporophytes. That is, these plants were the first to produce the structures called seeds. For a seed is merely a young sporophyte, produced by the microscopic gametophytes, within the tissues of the old sporophyte. It is evident that this system is much safer than that of the ferns, for the small gametophyte is safely housed instead of being exposed to the vagaries of the elements.

The Non-Swimming Sperms

Now let us see how sperm cells could be brought to this encased gametophyte within the tissues of the old sporophyte. It would be a simple matter to have the sperm cells swim through the contained moisture from one part of the little gametophyte to the other, but that would be self-fertilization and would bring little more advantage than transferring money from your right pocket to your left. Cross-fertilization appears to have become the dominant procedure. This means that the sperm cell does not arise in the same plant that produces the egg cell, and so, somehow, sperms must be brought to it from another plant. The first steps toward a more efficient fertilization technique are apparent in a plant previously mentioned, the clubmoss *Selaginella*. Here two sizes of spores are produced, and these give rise to two kinds of gametophytes, one male and the other female. Both of these show a high degree of reduction or degeneration. The larger *megaspore* gives rise to a simplified female gametophyte. The smaller *microspore* gives rise to a still more degenerated male gametophyte, which has been reduced to nothing more than a cellular capsule containing sperm cells, and these are still flagellated swimmers. Thus the spore-like gametophyte can serve the purpose of transportation through the air. If it then lands near a female gametophyte, it discharges its still primitive flagellated sperm cells onto the film of moisture surrounding it, thus continuing to rely on the ability of the

male gamete to swim to the archegonium.

In primitive seed plants, like certain cycads, the transition from swimming sperm has been almost but not quite completed. Note what happens. The female megaspore is retained within the tissue of the old sporophyte. A male microspore — now to be called a *pollen grain* — drifts through the air from another plant and may land on the sporangium which contains the germinating megaspore. As the latter germinates and mitotically develops into a female gametophyte, the microspore also germinates. The male gametophyte thus produced from the microspore is even more degenerate than the female one produced from the megaspore, for it is no more than a slender tube — the *pollen tube* — which grows into the tissues of the female sporangium. Meanwhile shrinkage of tissues in this megasporangium creates a chamber above the archegonia, which contain the egg cells. The pollen tube grows into this chamber and bursts, discharging two relatively huge, spirally ciliated and hence motile sperms which have developed within it. Here, although the male gametophyte has evolved in such a manner as to grow virtually all the way to the female gametophyte, the last small lap of the journey is still covered by a traditional swimming sperm in the traditional manner. The resulting zygote develops into an embryonic sporophyte while still housed within the sporangium of the old sporophyte, and thus a true seed is achieved.

Seed Plants: The Final Step

Although many refinements are still to be added in the seed plants by way of seed protection and dispersal, there is only one step to the kinds of gametes and fertilization characteristic of modern seed plants, and it is a relatively small one. This is the reduction of the swimming sperm cell to a mere sperm nucleus, incapable of independent motion, which drifts down the pollen tube to enter the egg cell. The microspore is the *pollen grain*, the male gametophyte the *pollen tube*, and the female gametophyte the *embryo sac*. Further details regarding this mechanism must be re-

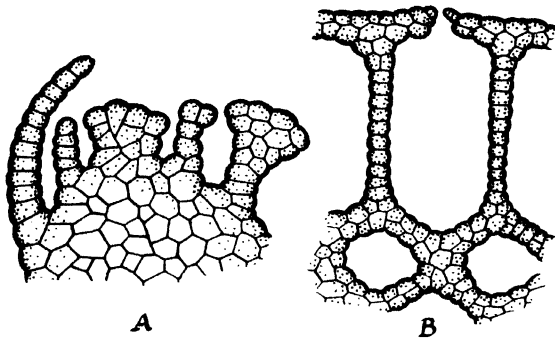


Fig. 145. Thallus of *Ricciocarpus*. *A*. Section during growth. Apical cells form columns or plates with air spaces between. *B*. Air spaces in older thallus are larger, and plates have roofed them over, leaving small pores for gas exchange.

served until we arrive at a study of the seed plants. The peculiar procedures that take place in the production of a seed would be all but meaningless without some previous knowledge of the reproductive processes in simpler plants.

LIVERWORTS AND MOSSES: (BRYOPHYTES)

The migration of plants from water to land brings us to the third great plant group, the phylum *Bryophyta* (Gr. *bryon* = moss). These are the primitive liverworts and their relatives,

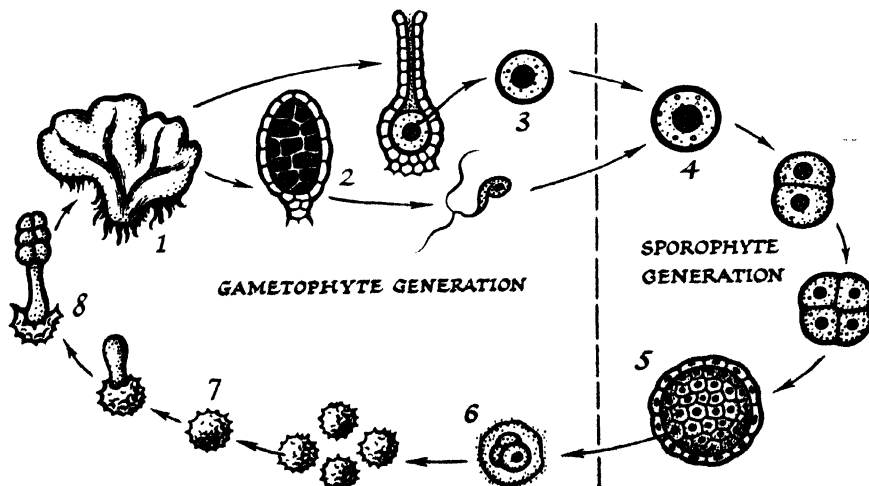
the more highly developed mosses, whose reproductive structures we have already mentioned. Unlike the loosely knit phylum *Thallophyta*, the bryophytes are a homogeneous group of plants rather indifferently adapted to life on land. Among them are some of the earliest land plants, suggesting almost diagrammatically the transition from the algae. The evolutionary relationships of the group are rather uncertain, though it appears that the phylum may represent an independent offshoot from primitive algae, an offshoot which led no further. Yet the rather awkward adaptations to land life of the bryophytes are suggestive and instructive.

The Liverworts

The liverworts, class *Hepaticae* (Gr. *hepar* = liver), derive their somewhat unattractive name from the fact that the thallus of the plant resembles the lobed form of a liver. Although the least known of the bryophytes, these are perhaps the most interesting in that they show early stages of adaptations which were much improved in higher plants. Two members of the group will illustrate.

Ricciocarpus. The first of these (Fig. 145) is extremely primitive, being merely a simple lobed thallus strongly reminiscent of the higher algae, though its cellular structure displays

Fig. 146. Life cycle of *Ricciocarpus*, a primitive liverwort. 1. The plant (the gametophyte) corresponds to the prothallus of the fern or the green moss plant. 2. Archegonium and antheridium with sperm cells and ova. 3. Egg and sperm. 4. Zygote in division. 5. Sporophyte, a rudimentary structure, consists mainly of spore mother-cells. 6. Spore mother-cell dividing to produce haploid spores. 7. A spore. 8. Spore germinating by cell division to become a gametophyte.



marked adaptations to land life. The whole plant may be likened to a single leaf, with a fuzz of colorless rhizoids or primitive roots projecting from its lower surface. The cells of this surface are compact enough to be a fairly strong base for the more loosely packed green cells of the upper surface, which are markedly adapted to their function. For instead of forming a compact green surface, they grow up in separated columns, forming walls. Under a microscope the surface of the thallus looks somewhat like a field covered with a pattern of closely set crisscrossed stone walls. Such an arrangement greatly increases the surface of the leaf exposed to air and hence its efficiency in the gas exchange of photosynthesis. The tops of the walls flare out laterally until they almost touch, leaving only small pores. The whole body, with its breathing pores, is much like the leaf of a higher plant, except that in the latter there is much greater refinement, as in the ability of the pores to open and close. Yet in both, the pattern of the leaf is such as to assure a large surface of green cells in contact with air for photosynthesis, yet protected against mechanical injury and dehydration by one or more layers of sturdier cells while air contact is maintained through the pores.

The remaining nutritive functions, absorption of water and minerals, and transportation of these substances and of synthesized compounds from one part of the plant to another, are carried on much as in the thallophytes. The rhizoids absorb water by osmosis, and transportation is by diffusion within cells and osmosis between cells. Beginnings of specialized conducting cells, although found in some of the higher algae, do not appear in land plants until we come to the mosses, while in the ferns there are real conducting tissue, consisting of tubes and ducts.

The reproductive cycle of *Ricciocarpus* shows a rudimentary form of the sporophyte phase (Fig. 146). The sporophyte generation which develops out of the zygote consists of nothing more than a spherical group of spore mother-cells, that is, cells which by further division

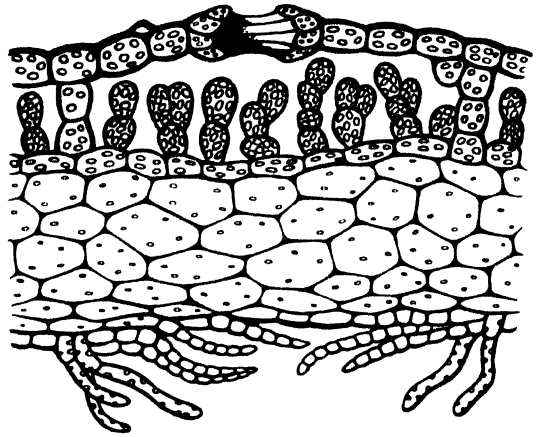


Fig. 147. Thallus of *Marchantia*, in section. Epidermal cells at top with pore above chlorenchyma. Below are rhizoids and scale-like plates.

become spores. Only in view of what we know about reproduction in the true mosses is it possible to call this ball of cells a plant. But its position in the reproductive cycle indicates that it is the counterpart of the slender stalk-like sporophyte of the moss plant and of the dominating fern plant itself. In *Ricciocarpus* the gametophyte is the dominating phase, and the sporophyte is hardly more than a proliferation of the zygote.

Marchantia. In both structure and activity, this plant proclaims its higher evolutionary standing. Though it is similar in form to *Ricciocarpus*, a cross section through its thallus shows considerably greater differentiation and specialization (Fig. 147). The delicate *chlorenchyma*, the photosynthesizing green cells, are well protected by the epidermis, the outer layer of protective cells, while ample air spaces surrounding these green cells communicate by flue-like pores with the air outside. But the base of the thallus as well as the rhizoids shows no marked improvement, and there is still no stem.

Reproduction in *Marchantia* approaches the sporophyte-gametophyte relationship of the moss plant (Fig. 148). The process is somewhat complicated because the thallus-like gametophyte produces odd umbrella-shaped structures bearing the archegonia and anther-

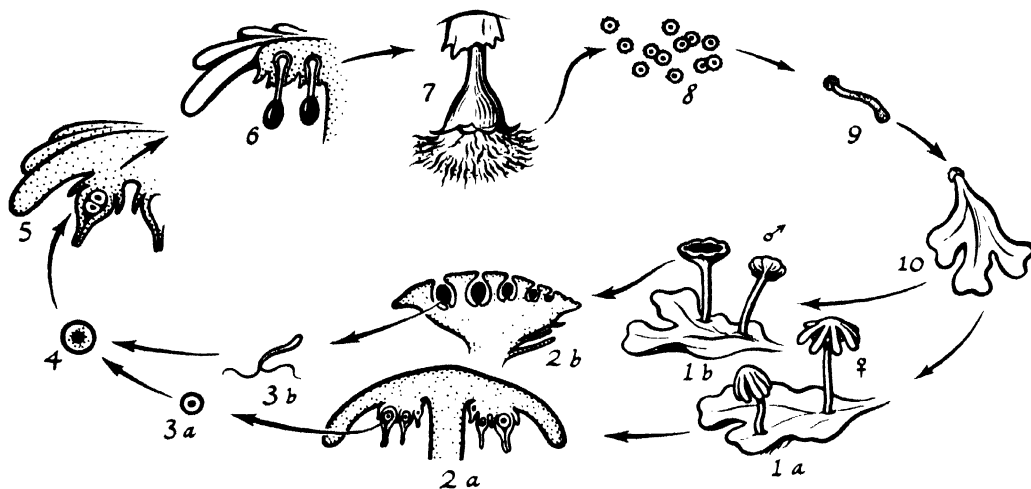


Fig. 148. The life cycle of *Marchantia*. 1. Male and female gametophytes. 2. Male and female gametophores (enlarged) with archegonia and antheridia. 3. Sperm and egg cells. 4. Zygote. 5. Zygote undergoing cell division within the archegonium to give rise to a new sporophyte. 6. Parasitic sporophytes growing out of the archegonium on the gametophores. Sporophyte consisting primarily of a stalk bearing a spore capsule. 7. Sporophyte (enlarged) growing from archegonium. The spore capsule has opened and fibrous structures called *elaters*, which help to distribute the spores, give a powderpuff effect. 8. Single-celled spores. 9. Early stages of spore germination. 10. Young gametophyte.

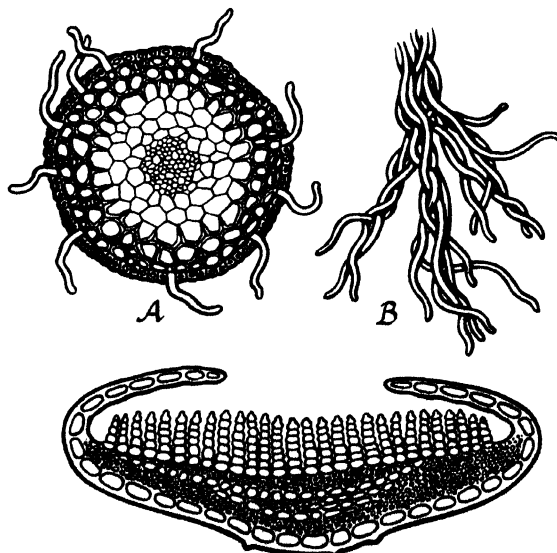
idia. The ovum, growing within the archegonium of a female plant, is fertilized by the sperm cells produced in the antheridium of a male plant. Fertilization occurs while the umbrella, the *gametophore*, is still a bud. As it grows, the zygote within its archegonium develops into a club-shaped sporophyte and eventually produces many spores which are assisted into the outer world by hair-like absorbent structures called *elaters*. Thus the sporophyte has become a clearly recognizable parasite attached by a root-like foot to its mother-host and with various accessory tissues that perish, after it has housed and scattered its spores.

The True Mosses

The plants of the class *Musci* (Lat. *muscus* = moss) show a distinct advance over the liverworts (Fig. 141). The gametophyte, still the dominant phase of the cycle, is the main moss plant itself. It is often a sturdier plant, and at the same time more refined and less simple, than a liverwort. For it is not a primitive formless thallus, but has a distinct stem, equipped with rudimentary connecting tissue.

It also has leaves, which may vary from simple sheets of green cells, equipped with elongated conducting cells forming a mid-vein, to rela-

Fig. 149. Anatomical features of mosses. A. Cross-section through base of stem, showing rhizoids, cortical and central conducting regions. B. Wick-like strands of rhizoids. C. Cross-section of leaf of *Polytrichum*, with margins folded in to protect chlorenchyma. During drought the leaf may curl further, exposing only thick-walled epidermal cells.



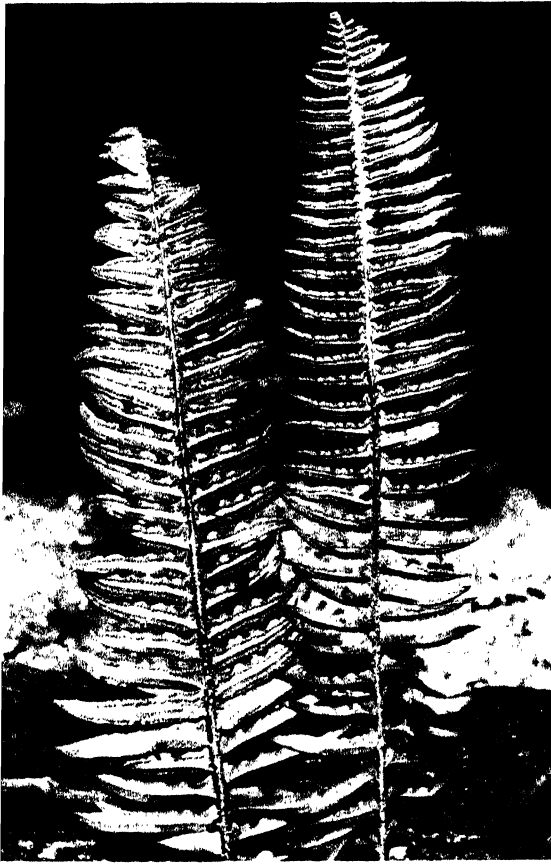


Fig. 150. The Christmas fern, *Polystichum acrostichoides*, common in North America.

tively complex masses of differentiated cells equipped for protection against drying. A root system is lacking, but the single-celled, hair-like root-hairs may be twisted together to form wick-like ropes (Fig. 149). Primitive though mosses still are, and intermediate in the degree of their adaptation to land life and in their mode of reproduction, they are probably a fairly recent offshoot from the liverworts, and are to be regarded as a limited and somewhat specialized form that does not lead to the higher plants of the present day. Absence of mosses in the early fossil-bearing deposits, as well as pronounced uniformity of structure within the group, are indications that they are possibly of relatively recent origin. Despite their divergence from the main path of evolution, especially noticeable in the in-

creased elaboration of the gametophyte, their structure and mode of reproduction are suggestive of the way plants became adapted to life on dry land.

THE FERNS: (PTERIDOPHYTES)

The fourth great plant group, phylum *Pteridophyta* (Gr. *ptēris* = fern, from *ptēros* = feather), so-called because of their usually feathery leaves, consists of the ferns and their close relatives.¹ Probably derived from algal ancestors by way of unknown intermediaries, and probably divergent branches of common types such as the trio *Rhynia*, *Hornea*, and *Asteroxylon*, the ferns show marked advances over these and the mosses in a variety of ways. Not only is the alternation of generations fully developed in the ferns, but they are all vascular plants with ducts or tubes for the transportation of foods, water, and raw materials. These structures, which will be discussed in Chapter 12, have made possible all the larger plants of today. Moreover, all the pteridophytes have leaves supplied by vascular bundles, although the form and arrangement of the leaves differs greatly in the various groups.

Despite these similarities, the three classes of pteridophytes — the clubmosses, the horsetails, and the true ferns — show considerable differences both in form and in reproduction. Again the random nature of evolution makes it difficult to feel sure which group should be considered highest in the scale, for in reproduction the clubmosses most nearly approach the seed plants, while in structure they are the least highly developed of all the pteridophytes. Indeed, the important thing to notice about any plant or animal group is not that it can be neatly placed at a given point on an imaginary scale of evolutionary “progress”; rather, that groups which are highly developed in one way may lag far behind in another, since life appears to be a process of accidental flow and change.

¹ See Appendix A for an alternative classification in which the ferns are grouped together with all other vascular plants in one phylum, the *Tracheophyta*. Either classification is acceptable.



Fig. 151. A clubmoss, the ground pine.

The Clubmosses

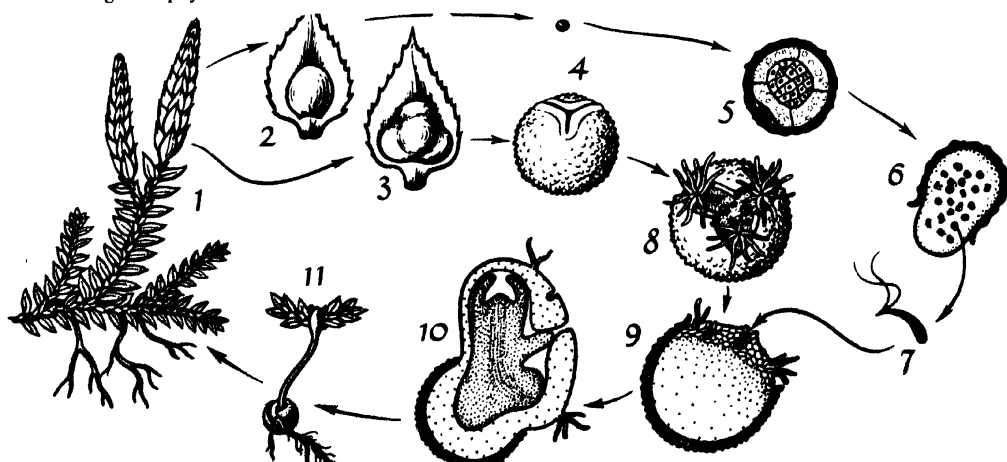
Though commonly known as clubmosses, the members of the class *Lycopodiineae* (Gr. *lykos* = wolf + *pod* = foot), such as the ground pine (Fig. 151), are really neither mosses nor pines. Largely tropical forms, they are the unimpressive survivors of a once great and dominant group of plants that flourished during the Carboniferous era. Some of these ancestral forms were large trees with trunks up to a hundred feet tall. The more efficient

seed plants have replaced them, and only their modest miniature descendants survive. One of the clubmosses, *Selaginella*, is of unusual interest because of its reproductive cycle.

Reproductive Cycle: *Selaginella*. It will be remembered that in the fern plant, the spore drops to the ground, germinates, and grows into an independent, small green gametophyte, in the archegonia and antheridia of which ova and sperms, respectively, are produced. When the ovum is fertilized, it grows into a young sporophyte which quickly emerges from the housing of the archegonium, sends out its own roots and shoot, and grows into an independent sporophyte again. This is the reproductive cycle of the fern. But in the seed ferns (pteridosperms, now fossil) the spore was retained in the sporangium and there became a parasitic gametophyte which produced ova while still in the position of the original spore. There fertilization took place, and there a new sporophyte was produced, encased in the tissues of the old one. Such a formation is called a seed.

Now look at the reproductive method of *Selaginella* (Fig. 152). Special shoots, called *strobili*, are formed on the main shoots of the plant. These have leaves like the other shoots, but on the strobilus each leaf, called a *sporo-*

Fig. 152. The life cycle of *Selaginella*, a club moss. 1. Portion of mature sporophyte with two strobili. 2. Microsporophyll, with microsporangium which produces many microspores. 3. Megasporephyll, with sporangium containing four megaspores. 4. Microspores (above) and megaspore. 5. Enlarged view of sectioned microspores, with reduced male gametophyte within. 6. Vertical section of mature male gametophyte, with sperm cells. Microspore case has split open. 7. A sperm cell. 8. Mature female gametophyte bursting the megaspore wall. Rhizoids and the necks of archegonia are visible. 9. Sectioned megaspore with two archegonia. 10. Embryo sporophyte in archegonium. 11. Young sporophyte growing out of gametophyte.



phyll, protects the sporangia placed in its axil, that is, at the point where it joins the shoot. Look closely and you can find two kinds of spores, larger megaspores and smaller microspores. Thus far there is nothing unusual about the situation. But there is a really unusual feature in the fact that the megaspore begins to germinate even before it has attained its full size, and so becomes a many-celled gametophyte before it is discharged from the sporangium. Note that the gametophyte is here a parasite on the sporophyte, just the reverse of the situation in the moss plants. After the gametophyte has fallen to the ground, the spore wall which still surrounds it ruptures, exposing it with its archegonia and ova to the swimming sperm cells. These have been liberated from a cellular sphere filled with sperm cells, the male gametophyte, which has meanwhile developed from the microspore and fallen to the ground likewise. The zygote then develops into an embryo sporophyte, which may have a resting phase within the gametophyte if outside conditions are unfavorable. In some forms, the gametophyte may even produce an embryo sporophyte before the spore is discharged from the sporangium, thus approaching even closer to the nature of a seed. The embryo sporophyte continues its growth, that is, it germinates, and a new plant arises from it, quite as a new plant arises from a germinating seed.

The advantages of this type of gametophyte formation are quite apparent. Further reduction in the size of the gametophyte would be hazardous, since at best it is vulnerable and at the mercy of changing environmental conditions. The hazard has been largely removed in *Selaginella*, despite the minuteness of the gametophyte, because the old sporophyte gives it enough nutritive material to carry it through its entire functional life, even in the total absence of light. The entire burden of providing for the next generation has been removed from the feeble gametophyte and now rests upon the robust sporophyte.

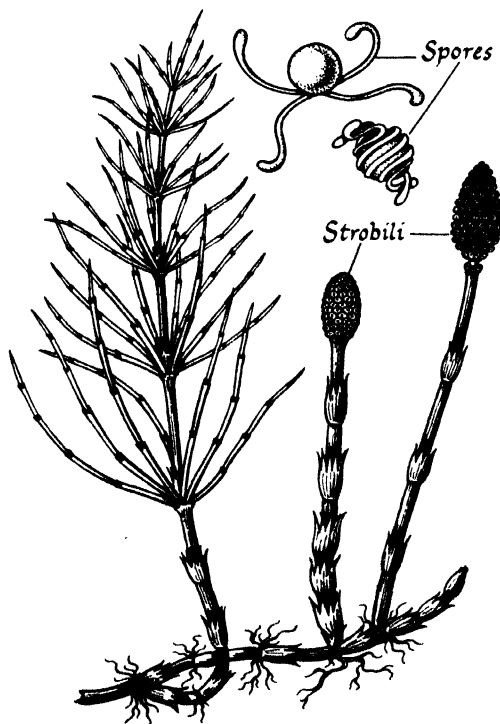
With the reproduction of *Selaginella*, we have traced the reproductive adaptation of plants

to land life almost to completion. Only the refinements of the seed plant remain. We have traced the transitional stages from the beginning of an alternation of generations to a strong gametophyte generation that supports feeble sporophytes. We have witnessed the continued growth of the sporophyte and the gradual suppression of the gametophyte, until finally in *Selaginella*, and still more in the seed plants, the gametophyte has degenerated to an almost unrecognizable structure parasitic on the robust sporophyte.

The Horsetails

The horsetails (class *Equisetinae*) are another remnant of a once mighty group. They are small wiry plants which look like miniature Christmas trees and grow on sandy, sterile areas and along railroad embankments. But in the era of coal bed formation, their ancestors were great trees rising to a height of perhaps forty feet. Today only a few tropical forms

Fig. 153. *Equisetum arvense*, the common horsetail. Sterile green branch (left) and fertile branches with strobili (right). Spores have spiral ribbons for dissemination (above).



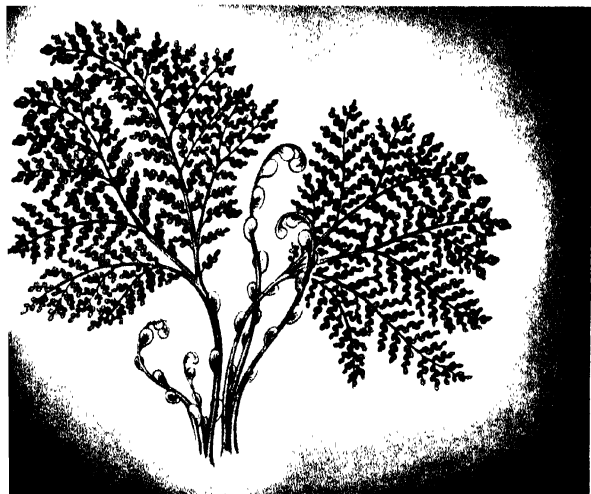


Fig. 154. A fossil pteridosperm or seed fern. The heart-shaped seeds may be seen attached to the fronds.

attain the height of small trees. Their general appearance has little to suggest their relationship to ferns but is so strongly reminiscent of the plants of the past that it is almost anachronistic (Fig. 153). The horsetails have lost the large green leaves of their ancestors, and only remnants of them remain in the form of whorls of scales. The stem itself has taken over the task of photosynthesis. The plant achieves a peculiar toughness because of the abundant siliceous deposits in its cell walls. It is for this property too that it was once called the "scouring rush," and was especially favored for the purpose of keeping pewterware bright. Sporangia are formed on special organs, the strobili. In some species, these appear on special reproductive shoots without chlorophyll and in others on the regular vegetative shoots. Here spores are produced and carried away by the wind, aided by peculiar ribbons, the elaters (Fig. 153). The spores develop into thallus-like gametophytes very similar to those of ferns, but of separate sexes. Whether they will produce antheridia or archegonia is determined by nutritive conditions, poor conditions causing the development of a small-sized male gametophyte. This is of unusual interest, since the spores of horsetails do not appear different in modern plants, although some fossil forms were heterosporous.

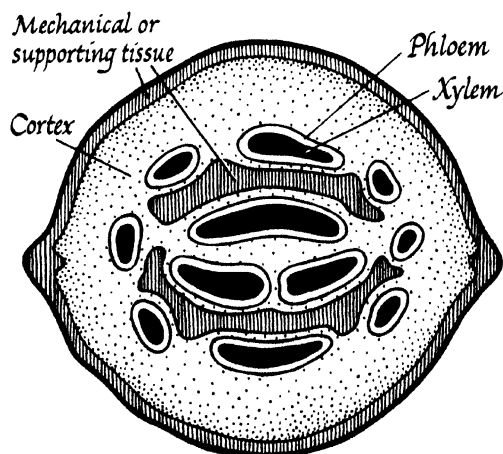
The True Ferns

The ferns, class *Filicineae* (Lat. = fern), are relatively recent offshoots of an ancient stock, but are not ancestors of the seed plants. Another offshoot of the basic fern stock, the pteridosperms (Fig. 154), may be considered a branch rather closer to the ancestral seed plants. Modern ferns are widely distributed over the earth, and despite the weak link in their reproductive system, namely, the independent prothallus with its swimming sperm,¹ many regions in the world today are suitable to this form of propagation. Compared with seed plants, however, ferns are a relatively unimportant group. Ferns vary in size from tiny plants to the tree-ferns of the tropics. All of them are characterized by the well-known fronded leaf which develops from the characteristically coiled "fiddle stem." The stems are usually prostrate — creeping, underground rhizomes — while only the leaves appear above the ground. Vascular bundles are well developed, as they would have to be to make possible the giant ferns of the tropics (Fig. 155).

Since the general plan of fern reproduction has been previously discussed, here we need observe only the structural details of their reproductive organs. Spores are produced on the ventral surfaces of the leaves. In some

¹ See pp. 201-202.

Fig. 155. Cross-section of fern stem. The specialized nature of the vascular tissue is evident.



species they appear on all the leaves; in others they are limited to lobes near the tips of the fronds. In still others, certain lobes of a frond are considerably modified sporophylls. In the sensitive fern, *Onoclea*, entire fronds are modified into non-chlorophyll-bearing sporophylls. In all these variations, the sporangia are arranged in groups or clusters and are protected by a sort of roof, or *indusium* (Fig. 156). This may be simply the curled-over edge of a leaf, it may be a peculiar umbrella- or toadstool-like shelter, or it may assume some other shape. Although the basic scheme remains more or less the same, the variations and modifications are unbelievably varied (Fig. 157). It is an excellent illustration of the shotgun method of nature in producing variant mutants, one or another of which is rather likely to hit the mark.

Thus, in the ferns, the obvious defects of the earliest land plants have been partly overcome. The dominant gametophyte of the liverwort *Ricciocarpus* corresponds to the dwarfed gametophyte of the fern. The spherical bundle of spore mother-cells of *Ricciocarpus*, representing its brief sporophyte generation, has in the fern become the glorified and dominating fern plant itself. There has been a complete shift in emphasis from the gametophyte to the sporophyte, a process which is carried even further in the seed plants.

EVOLUTION IN VEGETATIVE STRUCTURES

Structures that make it possible for a plant to survive on land had been evolved by marine species, especially those of the tidal zone. Even in certain early water plants we found flat thallus structures, rudiments of a vascular system, and root-like structures. Except under unusually favorable (that is, moist) conditions, these structures were a prerequisite for survival, or at least for further development, on land. In some of the very first plants, the entire plant body served the function of a leaf, as in the primitive liverworts. For further increase in size, however, an augmented system for the absorption of sunlight was essential,

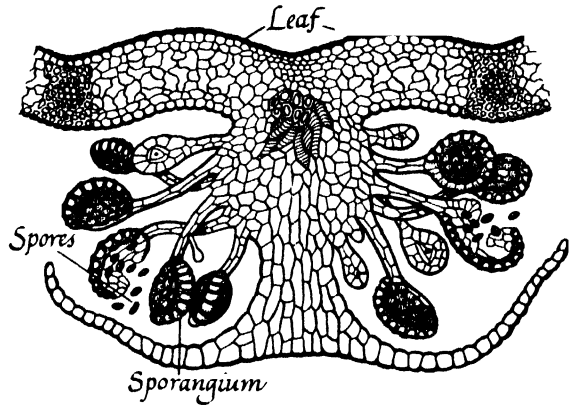


Fig. 156. Section through spore-bearing fern leaf. The inverted umbrella-like indusium protects the sporangia on the under side of the leaf.

and those plants which evolved it spread over a wider territory. Thus the true mosses had leaves of varying degrees of complexity. Leaves were most efficient when provided with a means of controlling water loss and with a direct connection to the water-absorbing regions, the roots, by a vascular system in the stem. The most successful method of controlling water loss was that in which the photosynthetic cells were surrounded by relatively coarse and waterproof cells but maintained their contact with the air by means of stomata or pores which could be opened or closed.¹ Such improvements were found in the more primitive club-mosses, although beginnings had been made as early as *Rhynia*, *Hornea*, and *Asteroxylon*. The vascular system of the first land plants, like that of ferns today, consisted of concentric bundles of two types of elongated cells, the heavy-walled woody cells, called the *xylem*, and the thinner-walled cells, called the *phloem*. In *Asteroxylon*, as in the fern, the phloem surrounds the xylem, and together they produce a central cylinder or strand. Since bundles of this vascular tissue branch off regularly to enter the leaves, this simple arrangement may become quite complicated, and at any one level separated bundles of such tissue may be scattered through the stem. Basically, the

¹ Fig. 192, page 240.

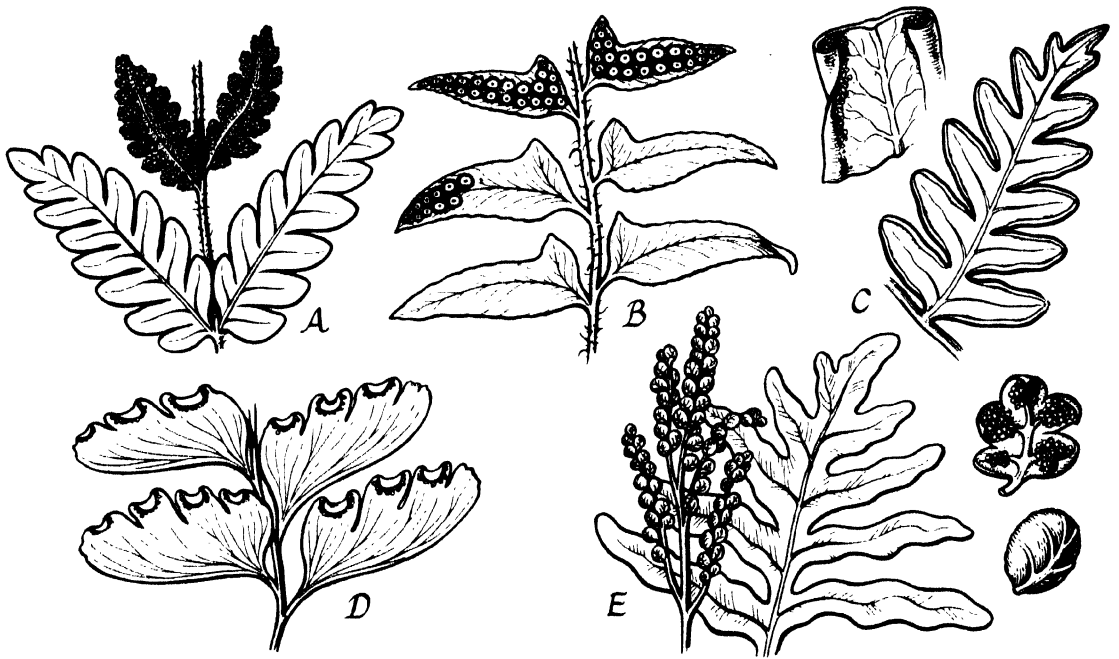


Fig. 157. Patterns of sporangium distribution in various ferns. *A. Osmunda*, the "flowering" fern. *B. Polystichum*, the Christmas fern. *C. Pteridium*, the bracken fern. *D. Adiantum*, the maidenhair fern; sporangia at the ends of leaflets are covered by rolled leaf-tip. *E. Onoclea*, the sensitive fern, produces its spores on separate specialized leaves; the berry-like structures are leaflets rolled around groups of sori on their under sides.

vascular system and the leaf structure are quite similar to those later found in the higher plants, as will be shown in Chapter 11.

Summary

The amphibious plants, liverworts and mosses, and the ferns, have often been regarded as illustrating the probable nature of the links in a chain of evolutionary events. We must not forget that no present-day plants could possibly be the real links in such a chain, since

they can hardly be the direct ancestors of other living forms, but rather are offshoots from the main branch. Still, they often retain a good many of the primitive characteristics of the real ancestral forms, and so shed light on what these must have been. Thus, as we have seen, the bryophytes and pteridophytes of today resemble in many interesting ways the plants which first invaded the land back in Silurian times, nearly 400 million years ago. And in turn they foreshadow the seed plants, the highest living plant forms of today.

Full Conquest of the Land: The Seed Plants

Even as the first amphibious plants were establishing themselves along the muddy banks of streams, lakes and tidewaters, mutations which would eventually fit plants for life on dry land were already being selected. By the Devonian, about 300 million years ago, the early land-plants had established a firm beach-head, and great forests had begun to blanket the earth. Judging by the extent of these forests, the early horsetails and clubmosses appear to have been magnificently successful, but they still had many shortcomings which left the way open for the ultimate domination of the seed plants, the *Spermatophyta*, the plant phylum which today is by far the most successfully adapted to the conditions of life on land.

Perhaps the chief weakness of the ferns, horsetails, and clubmosses was that the life of the species still hung on a vulnerable free-living gametophyte. Since the sperm cells still had to swim to the eggs, there had to be a continuous film of moisture, at least periodically, if the life cycle was to be completed. The agent of dissemination was still the small spore with limited food resources, so that only the lucky one that chanced to fall in a suitable environment could survive. One early group, the seed ferns, developed seed-like structures which appear to have overcome the obstacle of dry-land reproduction, but they must later on have failed to keep up with more progressive competitions, since they have not survived. For instance, in these first forest trees the trunks were still rather weak, for the ability to grow continuously new layers of secondary wood had not yet evolved. The Cordaitales, which together with the seed ferns, the great horsetails, and the clubmosses, formed the bulk of the carboniferous forests, were tree-like leafy plants, re-

lated to the modern conifers. It was left for other seed plants, perhaps their descendants, to develop the combinations of adaptations which made them endure where these failed.

Yet the evolution of the seed plants must not be thought of as a simple, pre-planned, or direct process. There is evidence that many of the structures that have ultimately become established in modern seed plants were repeatedly and separately evolved in other now extinct types. Indeed, some of these primitive intermediates, in altered form, have survived into the present age, and shed some light on earlier phases which have not come down to us.

The seed plants are of two main kinds, the class *Gymnospermae* (Gr. *gymnos* = seed), so-called because the seeds are not protected by a housing ovary; and the class *Angiospermae* (Gr. *angeion* = enclosing vessel), the "flowering plants," in which the seeds are protected by the enclosing walls of the ovary. In numbers, variety, and range of adaptability, the flowering plants have far outstripped any other plant group and represent the highest phase of plant evolution on earth today.

THE NAKED SEEDS: (GYMNOSPERMS)

This ancient group, which includes the more primitive of the modern seed plants and some of their extinct ancestors, stretches back into the Devonian, some 300 million years ago, and still flourishes, as witness some of the great pine forests of the north. The gymnosperms are quite varied, and range from fairly primitive forms which look much like ferns to the most majestic of the giant evergreens. There are even some deciduous trees among them, that is, trees which seasonally shed their leaves. But they have no true flowers; these are found only

among the angiosperms. The seeds of the gymnosperms are borne on special shoots or strobili called cones, which represent only the primitive beginnings of flowers. Indeed, this is their distinguishing mark.

Primitive Types

The more primitive among the gymnosperms bear marked resemblances to the ferns and thus indicate their ancestry. This is true of both surviving and extinct forms. We have already mentioned the seed ferns (pages 202–203), which appear to have been the first to develop something like a true seed. This extinct group flourished from the Devonian to the Jurassic, and is considered ancestral to a second group of fern-like seed plants which survive today.

This is the order *Cycadales*, named for one representative type, the *cycads* (Fig. 158), which themselves trace back to the Permian and flourished in the Mesozoic, sometimes referred to as “the age of the cycads.” These plants somewhat resemble ferns but have advanced distinctly beyond the seed ferns, for while they have a crown of large, feathery fronds, they also have heavy unbranched stems (ovulate sporophylls) that closely resemble the regular foliage leaves and bear their ovules along the edge, as do many ferns (Fig. 159). In reproduction an airborne pollen grain from a “male” plant enters the rather large pollen chamber on the edge of this sporophyll, and germinates in the collected moisture within the chamber.

Fig. 158. A sago palm or cycad. The stiff fern-like leaves are borne on stocky unbranched trunks.

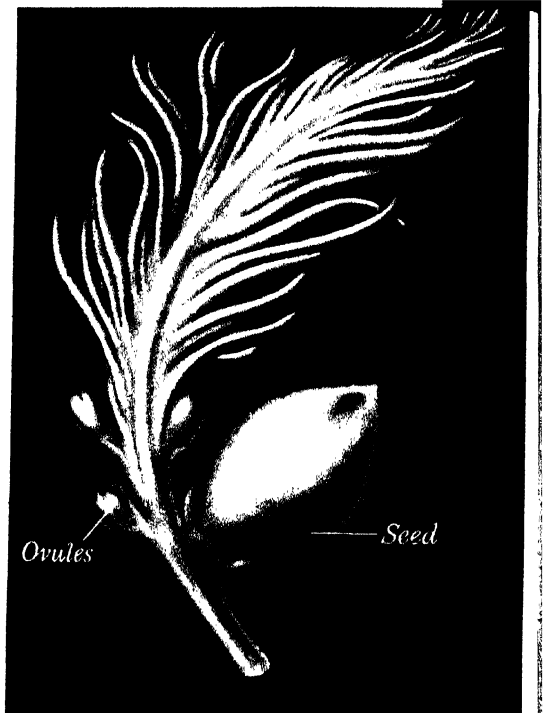


Fig. 159. Sporophyll of an ovulate cone of *Cycas*. Transformation into an ovule-bearing structure is incomplete, and the leaf still shows marked resemblance to the vegetative leaf.

The pollen grain develops into a fairly stout tube, the pollen chamber increases in size until it reaches the female gametophyte, called the *embryo sac*, and the end of the pollen tube bursts in close proximity to the archegonia. The two motile sperm cells are shaped somewhat like a top with a band of cilia spiralling around the pointed end (Fig. 160). There is nothing unusual about the swimming sperm cell; but its association with a pollen tube, a characteristic of all seed plants, and the fact that in the flowering plants the sperm has been reduced to a mere nucleus, passively carried to its destination by the pollen tube, shows that the cycad is an intermediate form.

Meanwhile somewhat less successful “experiments” were going on, in two other gymnosperm groups, one now extinct and the other still alive — only by accident, as it were. The first of these was the order *Bennettitales* (Fig. 161), whose members produced cones quite



Fig. 160. Male gametophyte of the cycad *Zamia*. The sperm cells are carried by a pollen tube, but are still motile, by cilia.

like flowers and may have been ancestral to the primitive angiosperms. Probably most of the cycad-like plants of the Mesozoic were members of this order. The second is the order *Ginkgoales*, represented today by only one living species, *Ginkgo biloba*, the maidenhair tree of China (page 164). No truly wild representative of this group has been known to exist for many generations, and it appears to have survived at all only because it was cultivated in and about the temples of China, whence it was introduced into Japan and finally into the western world. The tree has much the appearance of a modern angiosperm, though its structure is typical of the gymnosperms and it is distantly related to the cycads, for like them it has pollen chambers and motile sperm cells. Oddly enough, while it may owe its survival to the hand of man, the ginkgo has proved remarkably able to survive in unhealthy city environments.

Finally, two other minor orders show interesting advances in the direction of the seed plants. The first of these is the extinct *Cordaitales*, which flourished from the Devonian through the Carboniferous and together with the seed ferns formed all or nearly all the seed plants of the Carboniferous coal forests. These showed significant combinations of seed fern,

cycad, and conifer characteristics, but were not sufficiently well adapted to survive. The other group is the order *Gnetales*, which appears to lean toward the angiosperms in the structure of its wood and leaves and in its reduced female gametophytes, although the *Gnetales* produce the typical exposed seeds of the gymnosperms. These plants are highly specialized and bizarre. For instance, *Welwitschia*, a desert plant of western Africa, has two enormously long strap-shaped leaves that lie flat on the ground. *Ephedra*, from which comes the ephedrine used in nose drops, also belongs to this group. It may be that their very oddity — their extreme specialization — has limited their spread by limiting their adaptability.

The Conifers

By far the most successful of the modern gymnosperms are the conifers (order *Coniferales*, "cone-bearers"), the lords of their kind both in variety of species and in actual numbers. Typically they are much like the angiosperms in general structure, though they still reproduce by naked seeds, as shown in the pine tree, one of the most familiar representatives of the group.

Like all higher plants, the pine tree is a sporophyte upon which evolution has impressed certain sex differentiations — in this case *staminate* or "male" cones and *ovulate* or "female" cones

Fig. 161. Bennettiales "flower," restored. The "petals" are the microsporophylls. The megasporophylls are in the center. The cone resembles an angiosperm flower.

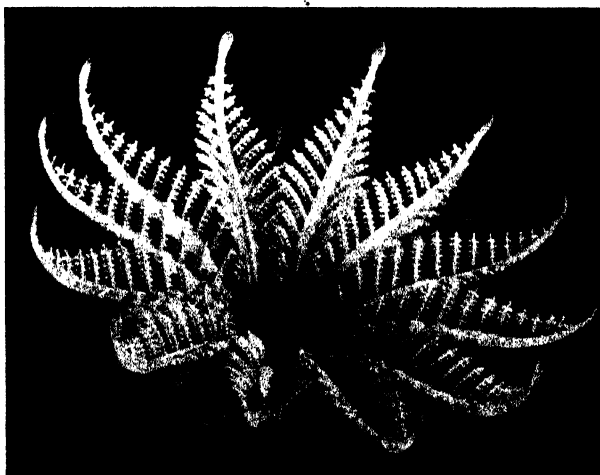
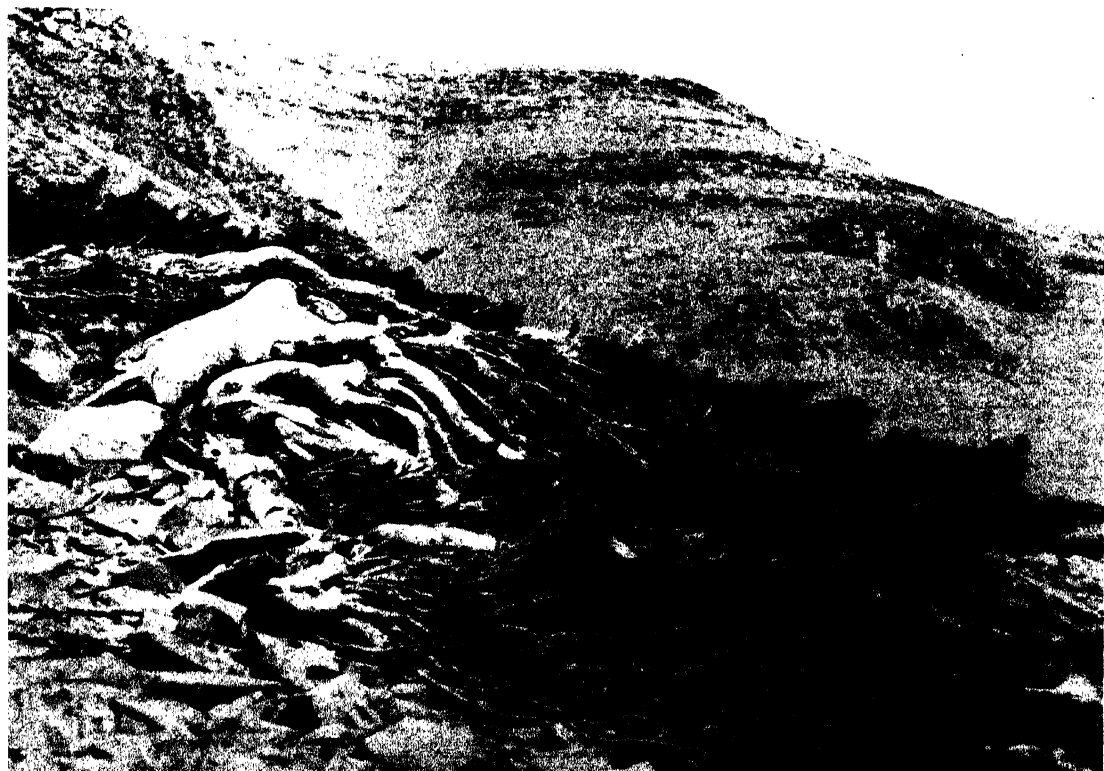




Fig. 102. Three conifers: Engelmann's spruce, piñon pine, and limber pine, all from western United States.

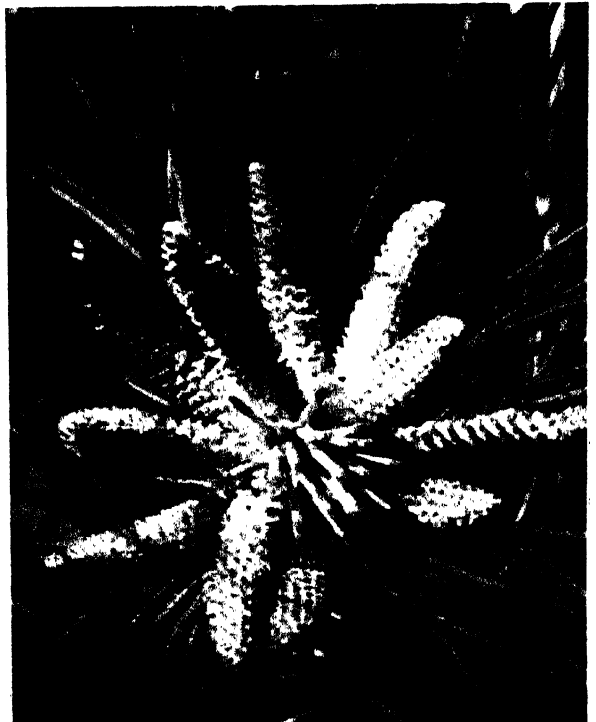


(Fig. 163). Early in spring, the small staminate cones grow in clusters at the tips of the branches and soon produce millions of microscopic cells, the microspores or pollen grains. Before these are liberated as thick clouds of pollen dust, they develop into an exceedingly degenerate male gametophyte, which has balloon-like projections for added buoyancy. If it is fortunate, the dust-like male gametophyte or pollen grain may land on the archegonium of a female gametophyte, which has developed from a megaspore within a female cone — the familiar pine cone, which during its first season stands erect and thus catches the pollen. Fertilization follows, whereupon the cones gradually droop. Another year passes, and the fertilized egg develops into an embryo pine within its covering. This is the seed.

Let us correlate these new structures with those found in simpler plants. To start with, in the male cone each microspore-nucleus divides twice, producing four nuclei, of which two degenerate. These may be compared to the body cells of the fern gametophyte. We may say, then, that the pine gametophyte has been reduced to two short-lived nuclei which would seem to have no function at all, were it not for what we know about other plants. The spore is now divided by a wall into a small generative cell, which contains one of the two remaining nuclei, and a larger cell, containing the *tube nucleus*. It is in this condition that the male gametophyte, the pollen grain, is carried to the ovulate cone. If it enters the opening in an ovule, in most cases a year elapses before the tube nucleus causes the cytoplasm to produce a long slender tube, and leads the way down this *pollen tube*, which grows down into the *nucellus* tissue of the megasporangium, of the female cone. Meanwhile the generative cell has divided again, producing a stalk cell, thought to be a vestigial antheridium, and a body cell. The latter, dividing once more, produces two sperm nuclei (Fig. 164). When the pollen tube finally reaches the female gametophyte, or *embryo sac*, one of these male nuclei enters and unites with the egg nucleus, while the other remains behind and



Fig. 163. Staminate (above) and ovulate cones of a pine. Similar cones, varying only in shape and size, are typical for the conifers.



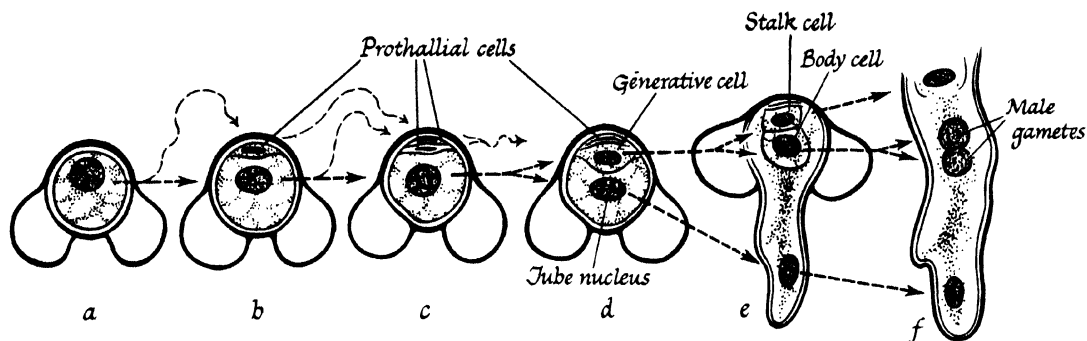


Fig. 164. Development of male gametes in the pine. Microspore, immature pollen grain, *a*, by a series of divisions produces two gametes, *f*, one of which becomes functional.

dies. Here, for the first time in our study of land plants, we see the swimming sperm cell replaced by a non-motile nucleus, transported through the agency of the growing pollen tube which itself makes contact with the female gametophyte. The impressive feature of the process is the seeming conservatism with which the plant clings to vestiges of certain established processes, such as the production of vastly reduced and apparently functionless gametophyte and antheridial cells, while at the same time almost completely eliminating the whole sexual organism — the male gametophyte — which has been reduced to little more than male nuclei and a tube to carry them to their destination.

The weakness of the pine in the struggle for existence is no longer to be found in a feeble independent gametophyte and a swimming sperm. If it has a clear weakness, that lies in the haphazard way in which the pollen grain must reach the pollen-chamber in the female cone, and perhaps in the lack of protection for the naked seed. Some of the angiosperms have evolved beyond these limitations, as we shall see.

THE FLOWERING PLANTS: (ANGIOSPERMS)

Evolutionary Ascendancy

The success of the angiosperms or flowering plants is clearly witnessed by their extraordinary diversity. In numbers, only the conifers approach them, and in variety, the conifers, and even the fungi, are far behind. Only in special and limited environmental conditions

have the lower plants been able to maintain a hold in competition with angiosperms. One quality that appears to have assured their success is their great adaptability, for some special type appears to have evolved in every sort of environment, so that they range from forest giants to the most delicate of herbs, from wholly aquatic types to the xerophytes of the desert. Besides, the flower and seed type of reproduction offers a greater chance for survival than do any of the methods found in lower forms of plant life. Indeed, the chief advances of the angiosperms over the gymnosperms lie in the refinement of reproductive structures and in the modification of the vascular system. To be sure, not all angiosperms have evolved that mutual relationship with insects which is one of the chief mechanisms of reproduction in true flowers, but this is only another example of the fact that evolution and survival do not guarantee a high degree of perfection in all characteristics of every plant. Some of them are primitive in certain respects and highly developed in others, a condition which is to be observed in all the organisms we have so far studied.

Contrary to general impression, the woody stem or trunk which is commonly thought of as a distinguishing characteristic of some of the most highly developed plants is not a recent development. Geological records tell us that most of the earlier seed plants had woody stems. Nor does this evidence imply merely that woody stems are more likely to be preserved than herbaceous ones, for many records of small and soft plant tissues have also been pre-

served. Soft herbaceous stems, which first appeared in the Cenozoic, probably represented an adaptation to colder climates, since the herbaceous stem can be sacrificed annually while the subterranean portions of the plant survive the winter. In modern plants woody stems are dominant in the tropics, while the herbaceous forms flourish in temperate zones. Where plant families contain both types, the herbaceous members are largely confined to temperate regions. It is interesting that the gymnosperms include few herbaceous forms, and that in angiosperm families where both are found, the herbaceous ones have the more advanced types of blossoms. Moreover, in the seed plants with the most highly developed flowers, the Sympetalae, many more have herbaceous stems than in the more primitive-flowered Archichlamydae. Perhaps in some distant future the forest giants of today may be looked upon with the mixture of awe and admiration that we of today bestow upon the dinosaurs.

The angiosperms are divided into two main groups, the *dicotyledonous* and the *monocotyledonous* plants, depending on the number of cotyledons, or embryonic seed leaves, produced in the germinating young plant. These leaves differ markedly from the permanent leaves produced later, and may be considerably modified for food storage. The monocots, which appear to have been evolved from simple dicots, include such groups as the grasses, palms, lilies, irises, and orchids. The dicots include most of the remaining angiosperms, such as the flowering trees and shrubs and most of the familiar garden vegetables and flowers. Within these two great sub-classes occurs all the extraordinary diversity of form and adaptive structure found in the angiosperms.

Reproduction in the Flowering Plant

One of the most striking adaptations among the angiosperms is the flower, and especially those sorts of flowers which have become adjusted to the services of insects. The parts of a flower are highly modified leaves and shoots

that have specialized in appealing to the sight and smell of animal organisms, and that is why we, with our animal senses, react so strongly to them. Where all earlier plants depended altogether on air or water currents for the dissemination of their reproductive structures, many angiosperms have made use of the various insects whose ancestors followed their own ancestors onto the land. The uncertainty of chance air currents has been replaced by the efficient delivery service of insects, some of which have in turn adapted their lives completely to the flowers they serve. No more highly perfected mutual adaptation can be found anywhere in the living world. Carrion flowers, so called because they are colored like carrion and smell like it, and carrion insects are adapted to each other's needs. The honey-bee fits as precisely into the mechanism of the nectar-producing snapdragon flower as one wheel of a watch fits into the next. The subtle devices of scent, color, and form by which the plant bribes the insect to transport pollen from one blossom to another are equalled only by the perfection with which the structure of the insect meets the precise needs of the flower.¹

The function of the flower is to aid in the transportation of pollen from one blossom to another. With what we know of the lower plants, we recognize the pollen grain as the spore, and pollination ~~not as~~ fertilization, but as the prelude to it. And as in the pine cone, we recognize the intricate processes that occur within the blossom, or ovulate strobilus, as representing the formation of the vestigial gametophyte.

The Flower. The flower (Figs. 165 and 166) is an extensive modification of the gymnosperm cone, with the added complication that microspores and megaspores are produced within the same flower. In a typical flower, a number of *stamens* (microsporophylls) within which the microspores or pollen grains are produced, surround the *carpels* (megasporophylls), within which ovules develop. These are the primary organs. The remaining parts of the flower are

¹ For a discussion of the insect portion of this relationship, see Chapter 16.

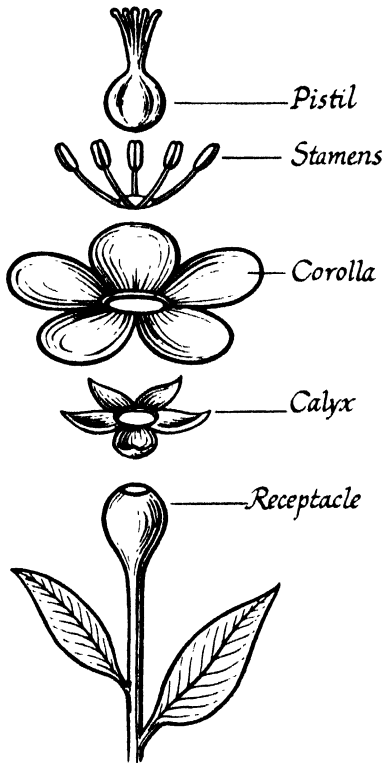


Fig. 165. Parts of a typical flower.

for protection and for advertising. These are the *corolla*, consisting of a circle of flower petals; the *calyx*, forming a circle of leaf-like sepals outside the corolla; and finally the base of the whole structure. Except for this last, all these structures are modified leaves. The one or more carpels each fold over, so as to form a small bag, usually so highly modified that its leaf-like structure is entirely obscured. Typically, several such chambers together form a flask-shaped container, the body of which is termed the ovary. The whole structure is referred to as the *pistil*. Within the ovary, the megaspores are produced, and within these form the female gametophytes. Fertilization of the egg and production of the enclosed young sporophyte which develops from it also occur here. In short, within the ovary grow the seeds.

The stamens look no more like leaves than a pistil does, though the water lily preserves

living evidence of their leafy origin (Fig. 166). The pollen-bearing part of a stamen, the *anther sac*, grows at the top of a *filament* and consists of highly modified tubular leaves within which the microspores or pollen cells are produced. Figure 167 shows a mature lily anther which is opening, thus exposing its spores for collection by insects. In such a flower, the leafy nature of the petals and sepals is apparent. In many flowers, however, these parts have been so changed and twisted that their origin is almost beyond recognition.

The Female Gametophyte

We return to the heart of a flower to observe the events that lead to the formation of an egg cell. Within the megasporangium or nucellus (Fig. 168), the megaspore mother-cell produces four megaspores, one of which grows while the other three degenerate. (The divisions

Fig. 166. Above: Separated petals of water lily show metamorphosis of petals into stamens. Petals are modified leaves, and stamens are petals further modified. Below: Longitudinal section of water lily, calyx outermost, then petals showing transition to stamens. Within are ovaries with curved style.



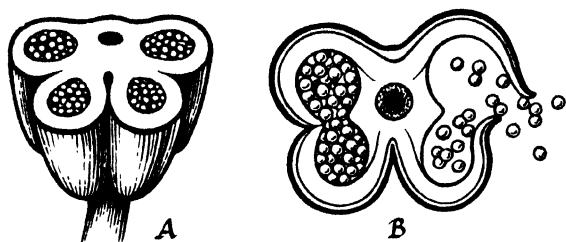


Fig. 167. Structure of the anther. *A.* The four sporangial cavities filled with spores. *B.* Mature anther opening to discharge spores.

producing these megaspores are the meiotic, or maturation divisions, and thus the diploid sporophyte produces a haploid megaspore.) By three later divisions, this time simply mitotic in character, eight haploid daughter nuclei are produced, which jointly occupy the cytoplasm of the cell, four at either end. One nucleus from each end then wanders toward the center of the cell, while the others become surrounded by cell walls which divide them from each other and from the remaining cytoplasm (Fig. 169). The nuclei which have wandered to the interior of the cell are the primary endosperm nuclei which produce those structures that will help to nourish the seedling. The entire eight-celled structure is the haploid female gametophyte, now called the embryo sac. One of the three cells at one end of the structure enlarges somewhat and becomes the egg, while its two companion cells, which perhaps assist in its development, may represent remnants of an ancestral archegonium, the flask-shaped egg container found in mosses and ferns. The three cells at the opposite end of the embryo sac will also disappear in the course of later development. This embryo sac, of only eight cells, is all that remains of the female gametophyte, corresponding in mosses to the main plant itself, and in ferns to the prothallus. In angiosperms the female gametophyte never sees daylight, for it passes its entire life buried in the ovary of the sporophyte seed plant, and it remains microscopic in size.

The Male Gametophyte

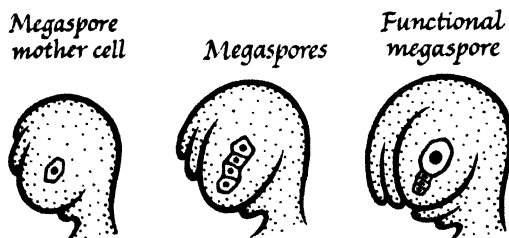
The simplification of the female gametophyte has gone far, but that of the male gametophyte

has proceeded even farther. In the anther the microspore mother-cell produces a typical quartet of haploid spores, each at first a single-celled pollen grain. The nucleus of this divides once to produce a generative cell and a tube-cell. (Note the simplification over what happens in the pine.) Now the pollen grain is ready to be transported to the stigma of a blossom, either by air currents or by insects (Fig. 169). There, nourished by the sugary solutions exuded by the tissues of the stigma, it grows into a male gametophyte. The procedure is very simple. Through pores in the thick-walled pollen grain, the tube nucleus directs the formation of a slender cytoplasmic pollen tube, which grows down through the tissue of the style until it reaches the ovary. Meanwhile the generative nucleus has divided once more, producing two sperm nuclei. These are the male gametes, while the pollen tube with its single tube nucleus is all that is left of the male gametophyte. The elimination of non-essentials could go no further without completely merging spores and gametes.

Fertilization and Seed Formation

Fertilization, the actual fusion of male and female gametes, occurs some time after the pollen grain has been transferred to the stigma and is distinct from pollination, that is, from the transfer of pollen to the stigma. It must also be remembered that the pollen grain itself is a spore (and then a gametophyte), but not a single gamete. The male gamete nucleus within the pollen tube is the actual sperm. When the tip of the pollen tube reaches an ovule, it enters the coats through a minute opening and, piercing the surrounding nucellus, makes contact with the female gametophyte. It penetrates the embryo sac too and then

Fig. 168. Longitudinal section of ovule showing development of functional megaspore.



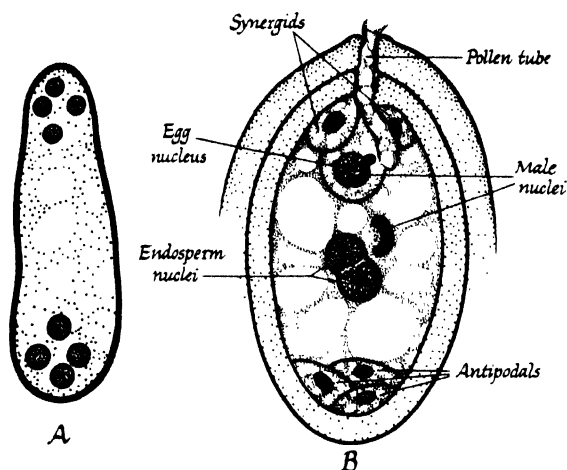


Fig. 169. Formation of female gametophyte (embryo sac) in seed plants. *A.* Young gametophyte with eight haploid nuclei produced by megaspore. *B.* Fusion of male nucleus with egg nucleus.

bursts, releasing its two sperm nuclei, one of which fuses with the nucleus of the egg, while the other wanders toward the center of the embryo sac and there fuses with both of the female endosperm nuclei to form a single *triploid* endosperm nucleus. The fertilized egg, or zygote, now becomes an embryo through repeated mitotic divisions. First it produces a string of cells, the *suspensors*. These push the remaining mass of cells, which is to become the embryo proper, up into the mass of the endosperm cells produced by repeated divisions of the original endosperm nucleus. In due time these processes result in the formation of a well-differentiated little plant with embryonic root, stem, and leaves, surrounded by food reserves and housed within one or more protective coats. This is the seed.

Seeds are of the most varied forms and patterns, and they strikingly demonstrate nature's variety. For all conceivable means of achieving some advantage for the organism may be found in the adaptations of seeds and the structure that houses them, the fruit. There are parachute seeds, as in the dandelion and milkweed; propeller or autogyro seeds, as in the maple and catalpa; hitch-hikers as in the cocklebur and beggar's tick; bribers, as in

tempting edible fruits such as blueberries, chokecherries, and others. Some seeds are catapulted into space by exploding seed pods, as in the touch-me-not, violet, and wild cucumber. Some are attached to rafts that float them to distant places, as in the coconut and lotus. Some seeds are specialized in staying power rather than in form. Anyone who has ever attempted to eradicate wild mustard from a field cannot withhold reluctant admiration for the persistence of this pest. Although an annual, it will appear and reappear as if by magic, even though each new crop of seedlings is promptly harrowed under. Mustard seeds may lie dormant for twenty years or more, perhaps plowed under by a previous generation of farmers. Brought back to warmth and air by a new plowing, they will germinate, assuring the survival of the species by the sheer staying power of the life they hold. Seeds of water lilies have been known to germinate after being buried for two hundred years in a Chinese peat bog. If seeds do all these things, it is little wonder that the angiosperms dominate the plant world today.

The Fruit

Not only does the sporophyte house and nourish the seed, it also develops a fruit to protect it and provide for its dissemination. The fruit consists of the ovary, sometimes enormously enlarged, and may also include other parts of the flower, as in the apple. With the exception of the seeds within it, the fruit is entirely a part of the parent plant on which it grows. The source of the pollen which cooperates in producing the seed usually has no effect on the nature of the fruit.¹ A McIntosh apple tree, for instance, will always produce McIntosh apples, no matter what variety of apple tree produced the pollen that pollinated the blossom. Yet the apple may house seeds of

¹ In some plants, as in corn, the endosperm produced in the double fertilization displays visible characteristics of the pollinating parent introduced by the male nucleus. This phenomenon is termed *xenia* (Gr. *xenia* = gifts of friendship).



Fig. 170. Various types of fruits. *a.* The pea, a dry fruit. *b.* The tomato, a fleshy fruit, is a berry. *c.* The wild cherry is a drupe. *d.* In the aggregate raspberry, each berry consists of many ripened pistils, all parts of a single flower. *e.* The multiple pineapple is produced from a compact inflorescence of many flowers. *f.* The strawberry is an accessory fruit.

greatly varying genetic constitution. This is because the ovary represents modified leaves of the tree itself, and it is the ovary which is transformed into the fruit. In short, the fruit represents an integral part of the system for seed preservation and dispersal; that is to say, seed dispersal is often accomplished by fruit dispersal.

Fruits are of many different types, but may be classified according to their structure as *simple*, *aggregate*, or *multiple*. Simple fruits are the product of a single flower. Among these are dry fruits as well as fleshy ones. The dry fruits include nuts, the bean or pea pods, and the grains of grasses, in which the seed coats are so fused with the ovary wall that the latter

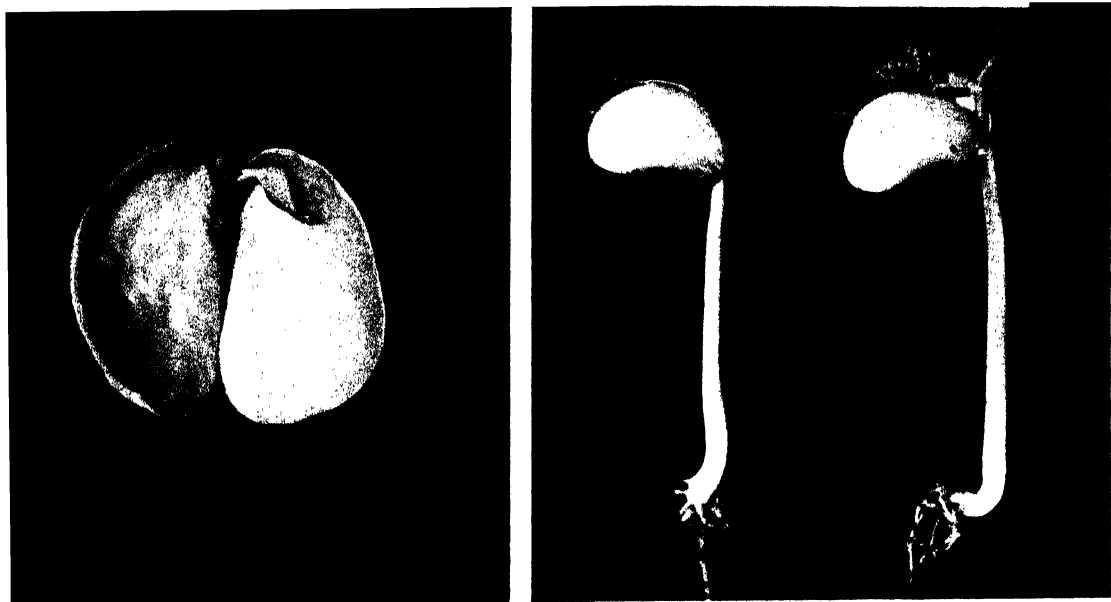


Fig. 171. Germination and development of bean seedling. Left: Split bean showing embryo. Right: Root, stem, and leaves. In this plant the cotyledons are lifted above the ground; in others, as in the pea, they may be left in the ground as the stem above them grows.

is difficult to recognize as a separate structure. Simple fleshy fruits include the berries, such as the gooseberry, grape, and tomato; the drupes, such as peach and cherry; and the pomes, like the apple and pear. A modified berry, called a *pepo*, is found in the watermelon and cucumber. Another sort of modified berry is the orange. Aggregate fruits include the raspberry and the blackberry, which are really clusters of pistils belonging to a single flower. The mulberry is a multiple fruit, formed from a number of closely clustered flowers. The strawberry consists of numerous one-seeded hard fruits clustered over the enlarged receptacle which forms the edible "berry." This is termed an *accessory* fruit.

The Seed

The seed which lies within the fruit may be single or multiple, depending on the nature of the inflorescence or flower arrangement that produced it. And the heart of the seed is the embryo, actually a miniature plant, surrounded with reserves of food and protective seed coats. Sometimes the minute pore through which fertilization took place may still be seen in the seed coats. Near it may also be seen the scar

left on the seed when it broke away from the stalk by which it was attached to the ovary during its formative and growing periods.

The more detailed structure of a dicotyledonous seed may best be observed in one of the larger seeds, such as that of a bean. If a bean is split, each half of it is seen to be an enormously overdeveloped seed-leaf or cotyledon, and hidden between the two cotyledons lies the embryo itself. The cotyledons are produced from the same cells as the rest of the embryo, but their function of food storage and early photosynthesis is restricted to the embryonic and seedling stages of the plant's life, and once having served their purpose, they die and are discarded. The remainder of the embryo is differentiated into two main regions, the *epicotyl*, which is a bud consisting of miniature neatly folded leaves and a growing point; and the *hypocotyl*, which is a combination of stem and root, also with a growing point. Not all dicotyledonous plants have such enormous cotyledons as the bean. In some, like the morning glory and the buckwheat, most of the reserve food is stored in the cells of the endosperm. Others exhibit all possible degrees of difference between these two extremes.

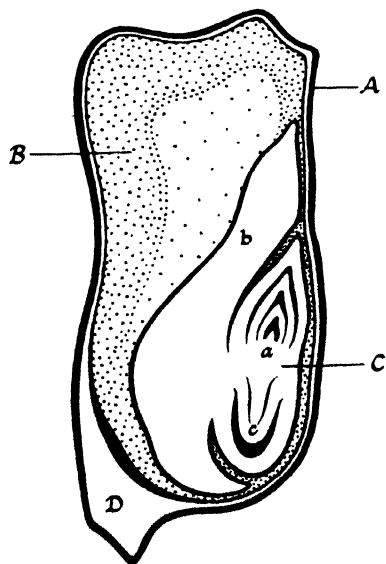
In the monocotyledons, the endosperm is always well developed and forms the bulk of the seed (Fig. 172). The embryo itself is a small flat flake at one side and end of the seed, and consists of a pointed flat structure, a single cotyledon, plus an epicotyl and hypocotyl like those of the dicotyledons. In any seed, the sporophyte which is to grow from it is already present as a miniature plant which, when it germinates, will merely continue the development and growth which has already started. In its stage of development, a seed may be compared to a hen's egg with a fully formed but miniature chick within it.

Germination of the Seed. The seed is a living, breathing thing, and it is dormant only in the sense that its metabolism has been reduced to a minimum. Under suitable conditions, it will germinate. That is, its metabolism will increase; it will release enzymes which transform the stored starch, sugar, or fat within the cotyledons or endosperm into a soluble form available for immediate use by the young embryo; and it will grow. What those suitable conditions are varies considerably from seed to seed. Some will germinate the moment there is sufficient moisture and satisfactory temperature. Others must go through a dormant period,

especially the seeds of wild plants and particularly those which, because of their vitality and persistence, we term weeds. This period of dormancy is of great value to the species, for it means that the plant does not gamble its existence on a single spell of favorable weather. Some seeds even have to undergo a period of freezing, which prevents them from germinating in warm fall or winter weather only to be killed by the frosts which follow. Moreover, a weed whose seeds all germinated at one time could easily be eradicated, for one tillage of the infested soil shortly after germination would eliminate the plant.

Whatever delaying factors may influence germination, all seeds require certain favorable conditions. They all require oxygen for growth, and if too deeply buried will not germinate, for lack of it. They need water, since protoplasm is largely water and needs water to produce more of itself. Water is also the medium in which soluble foodstuffs must be dissolved before they become available to the growing embryo. Yet too much water, by filling the air spaces in the soil and so decreasing its absorbing surface, reduces oxygen content and thus delays germination. Finally, a moderately warm temperature is necessary. The rate of chemical reaction increases with a rise in temperature, but a rise beyond a certain point causes death. Temperatures between 20° and 30° C. are generally most favorable.

Fig. 172. Longitudinal section of a corn grain, a one-seeded fruit. A. Grain coat. B. Endosperm. C. Embryo: a, epicotyl; b, cotyledon; c, hypocotyl. D. Grain stalk.



Early Growth

The germination of a seed is a vivid and dramatic event, but unfortunately too gradual for our impatient eyes to follow. But viewed by the time-lapse motion picture camera, it is unforgettable. First the hypocotyl drills through the protecting seed coats, and like the questing nose of a worm, twists and probes as it lengthens. This drilling motion, ideally suited to clear the way as the root tip bores through the soil, is achieved by changes in the rate of growth on opposite sides of the root. No matter what the position of the seed at the beginning of its germination, the root tip unerringly responds to gravity and grows down



Fig. 173. Seedling of radish, with root, covered by root hairs, extending downward.

into the soil (Fig. 173), and once there it responds to moisture by growing toward it. Light has an opposite effect on the root, which grows away from the light source. Such growth responses, *tropisms*, are either positive or negative, depending on the reaction.

Soon after the root has bored its way into the ground, the upper portion of the hypocotyl begins to elongate to form the stem. By now the swelling cotyledons have burst the seed coats, and the latter are lifted above the ground or left behind as the elongating hypocotyl twists the epicotyl through the soil by the same undulating and gyrating motions as in the growing root. The shoot or epicotyl responds to environmental stimuli such as gravity in an opposite manner to the root, and thus it grows upward. A cluster of seedlings viewed by time-lapse photography looks like a weird group of unearthly dancers performing some strange rite. After the cotyledons have reached the surface, the seed-coats, which have protected them until now, are finally thrown off by the further expansion and growth of the

cotyledons (Fig. 171). The plumule now unfolds, exposing the first true leaves to the sun, where they may begin photosynthesis. Meanwhile, growth has gone on with the aid of the sugar produced from the hydrolyzed starch of the cotyledons, aided by the enzymes produced by the growing embryo. Thus exhausted, the cotyledons shrivel, become limp, and eventually drop off. The root, during all this time, has continued its growth, and small bulges appear here and there along its side. These secondary or lateral roots begin the same drilling action as the main root. Near the growing tip of each root there soon appears a fuzzy growth of tiny root hairs (Fig. 173), which increase the absorbing surface of the root. Vascular bundles form as fast as the root, stem, and leaves grow, establishing networks of tubes and ducts for the substances which the plant absorbs and manufactures. The seedling has now become established. Growth and maturation will follow.

THE MATURE VASCULAR PLANT

The term *vascular plants* is applied collectively to the ferns and the seed plants because these two phyla have true vascular tissue for the conduction of water and nutritive substances. Because of similarity in structure and function, the typical angiosperm may be taken to represent both groups. Diagrammatically, a dicotyledonous plant (Fig. 174) is a series of three concentric cylinders with lateral branches above and below the ground. Combined, these cylinders form the body of the plant, which is divided into two main sections, the root and the shoot, the latter including the leaves. The structure of root and shoot are essentially the same. The tips are masses of undifferentiated cells responsible for the increase in the length of the plant. These are called the growing points. The bulk of the plant is represented by the central cylinder or *stele*. This is composed in the interior of loose, thin-walled cells, the pith, or primary axial tissue, which in turn is surrounded by fibrovascular bundles united by a more or less continuous layer of active growing tissue, the *cambium*. The fibrovascular

bundles are the conducting and supporting tissues of the shoot and root, and consist of the food-conducting tissue, or *phloem*, just under the bark, and the water-conducting and woody supporting tissue, or *xylem*. Surrounding the central cylinder is the second cylinder, the *cortical system*, which is green in young stems and at that time aids in photosynthesis, while in older stems it serves as a storage system. The third and outermost cylinder is the *dermal system*, which serves as a covering for the entire plant. It is this layer which produces the root-hairs and the protecting waterproof layer of the young stem and the leaf. In the leaves, branches of these three cylindrical structures give rise respectively to the vascular bundles (central cylinder), the chlorophyll-bearing tissue (cortical system), and the epidermis (dermal system).

Types of Plant Tissue

This pattern reveals one of the characteristic features of plant structure as contrasted with that of higher animals: namely, that the various tissues are more or less evenly distributed throughout the entire plant. A classification of tissues according to function is rather arbitrary, but four main groups may be established.

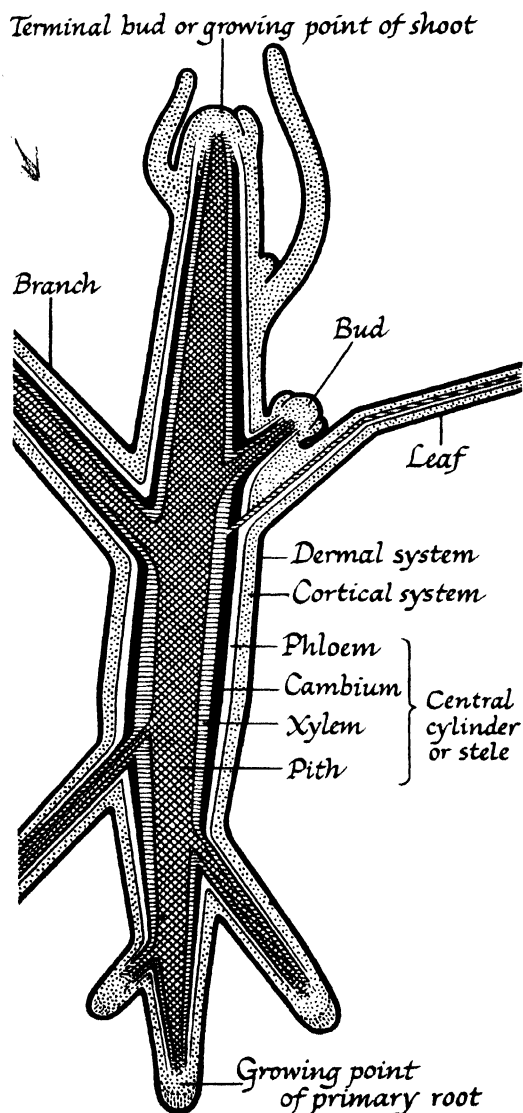
Meristematic tissue, which may also be called *embryonic*, makes up the growing points and the cambium. They are the growing cells of the plant, and all other tissues are derived from them by specialization and differentiation. These cells, typically small and thin-walled, are filled solid with cytoplasm and nucleus, whereas most other cells have large vacuoles and a relatively larger nucleus.

Fundamental tissue includes numerous types of slightly differentiated cells, among them those which form most of the soft parts of the plant, such as the leafy tissue, the pith, and the cortex. The least highly differentiated tissues in this group compose the *parenchyma*. Those which contain chlorophyll form the *chlorenchyma*, mainly in the leaves. Some cells within this group are surrounded by heavy walls and serve as supporting structures, the *sclerenchyma*, both in the bark and in the xylem.

Protective tissue forms the outermost layer of the plant. This is characteristic of the dermal system. Typically, this tissue forms layers one cell deep. Epidermal tissues may be thick-walled and relatively waterproof, as on the surface of the leaves, or they may be comparatively thin-walled, as in the roots, where they must permit diffusion of water and soluble substances.

Conductive or vascular tissue consists of highly

Fig. 174. Ideal vertical section of a generalized dicotyledonous plant. Each succeeding tissue layer is a hollow cylinder covering the layer beneath it.

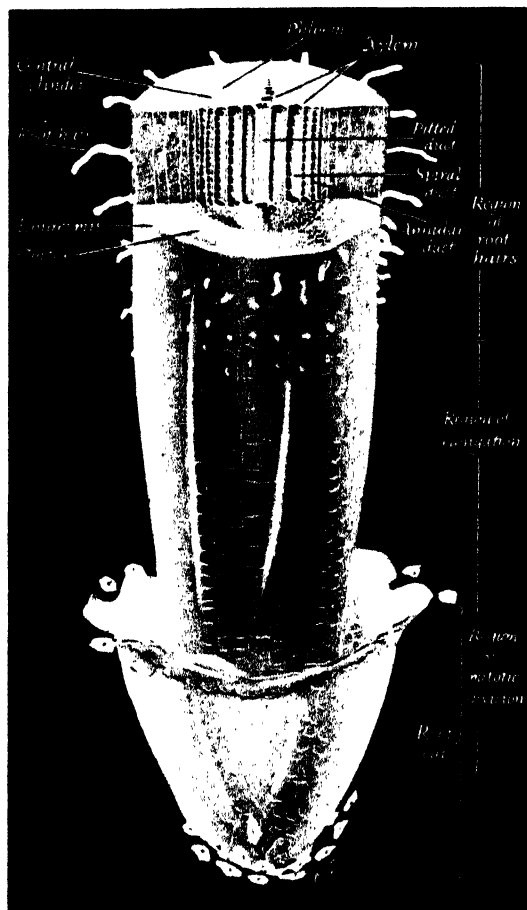


specialized cells forming the *sieve tubes* of the phloem, and the *ducts* of the xylem. Sieve tubes are characterized by peculiar perforated end-walls (hence their name) through which protoplasmic continuity from cell to cell is established, thus probably facilitating diffusion because no cell membranes have to be passed. The ducts are composed of mere remnants of cells, for after they have reached full development, the cytoplasm within them disappears, leaving only long continuous pipes for rapid conduction of water and dissolved salts.

Plant Behavior: Growth

In animals, all parts of the organism grow, but in plants the production of new cells is

Fig. 175. Section of a root tip. The zone of growth by cell division is within the root cap.



mainly limited to the meristematic tissue which makes up the tips of all growing points, such as the ends of branches and roots, and which also forms a continuous cylindrical layer, the cambium, beneath the phloem in roots and shoot. The contrast between such a method of growth and that of a typical animal may be visualized by imagining what a human being would look like if he grew in plant fashion. Appendages would increase in length only at their tip ends, while increase in girth would occur more or less evenly over the entire body. Finger tips, nose, toes, and the tips of the ears would appear and continue to increase in length only after the legs and arms had reached their final lengths. At the same time, these appendages would all constantly increase in thickness. The effect would be grotesque by human standards, but normal by the standards of the plant.

Growth in length is the result of cell divisions in the meristem of the terminal growing points. In most roots, the cells of the terminal meristem form new cells ahead of them as well as behind them (Fig. 175). Those ahead form the expendable root cap, which may be likened to a body of shock troops. These take the brunt of the punishment as the root pushes through the soil. The older ones eventually slough off and die. The cells which are split off back of the growing tip either form enduring somatic cells of the root, later to become differentiated, or they may retain their embryonic nature to form the meristematic tissue of lateral growth, the cambium. The meristem cells never change their nature; they remain young throughout the life of the plant. Hence, theoretically, there is no reason why a plant should ever stop growing. A woody plant eventually ceases to grow and dies probably because of other factors, such as a change in balance between tissues as the plant increases in size, or a reduced resistance to disease.

Conditions of growth are essentially alike in both root and shoot, except for certain complications that arise in the formation of structures such as leaves and buds. As in the root, the terminal meristem produces somatic cells, more meristem, and cambium. Unlike the stems,

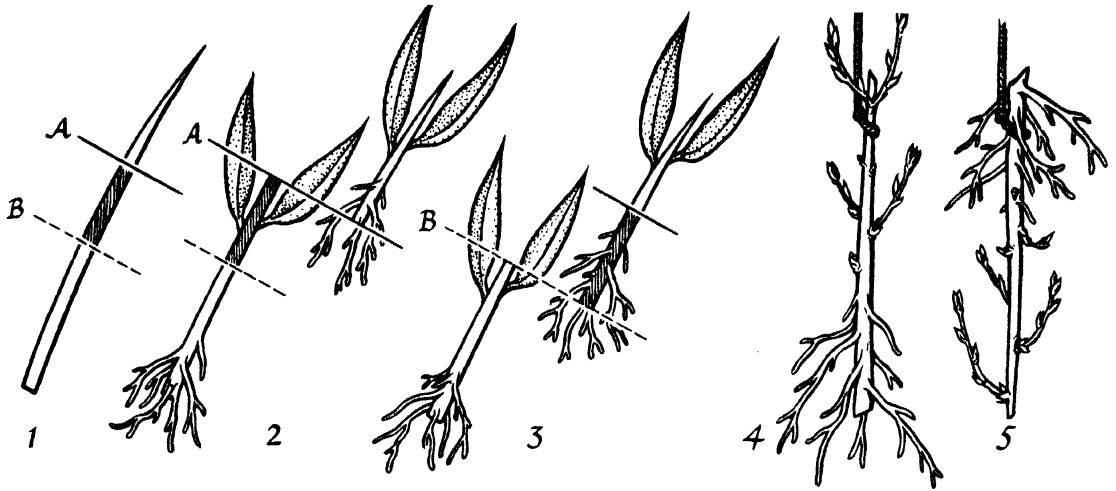


Fig. 176. 1-3. A willow branch produces leaves or roots, depending on whether it is cut at A or B. 4-5. A suspended twig will grow roots at the basal end and shoots at the apical, even if suspended upside down.

however, the leaf is an organ of limited growth, with no terminal meristem. Growth occurs through the temporary proliferation of meristematic tissue at the base of the leaf. Thus in both root and shoot, all differentiated tissues spring from the embryonic meristem which has been reproducing itself from the plant's earliest days. Hence the growing points of a thousand-year-old fir are no "older" than those of a year-old seedling. This may be shown by the fact that a twig clipped from an ancient and dying willow, if rooted, will grow into a young tree in no way handicapped by the "old age" of its parent.

Differentiation and Response

These facts raise many questions. We may ask why an entire root system can grow from a twig clipped, perhaps, from a hundred feet above the ground. Under ordinary conditions such a twig would eventually have become a stout branch, but certainly never a root. If we could answer this, we might also answer the more basic question put earlier: how does undifferentiated tissue become differentiated into many different kinds of specialized tissue? Experimental evidence sheds some light on these questions.

Polarity. If a willow branch is cut at a given point A below its tip and placed in a moist atmosphere (Fig. 176), the stump that remains

will send out new leaves, while the base of the cutting will produce roots. Had the same branch been cut a few inches farther away from the tip, at point B, roots would have formed at a level which in the first case remained a part of the stump and produced leaves. We may conclude from this that the relative position of cells with respect to the rest of the plant-body must have something to do with what they are to become. Roots always develop at the basal end of the cutting and leaves from the apical end. If we suspend another twig under the same conditions, base up, roots will still grow from the basal end, even though it is now uppermost, while leaves will sprout from the apical end, now below. Twigs of "weeping" or pendent varieties of trees show the same polarity, for the twig will grow roots at the basal point, nearest the tree, despite the fact that it was the uppermost portion of the branch while it was still attached to the tree. This and other experiments show clearly that there is a *polarity* of some sort within the plant tissue.

Auxins. Polarity is also found in animal tissue, and is probably due to chemical gradients from cell to cell, although electrical polarity may also be involved. Such a chemical gradient may be compared to the condition found in a bottle of milk. Soon after it is thoroughly mixed, cream will rise to the top, and

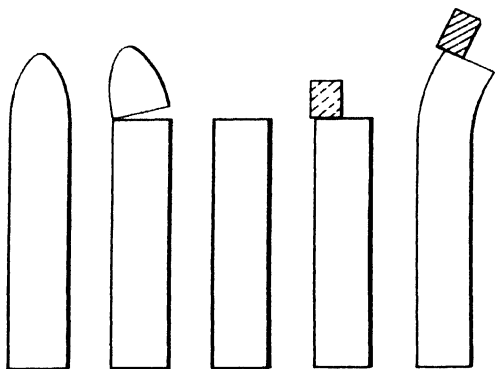


Fig. 177. Effect of growth hormone on decapitated oat shoot touched on one side of the stump with gelatin containing the hormone.

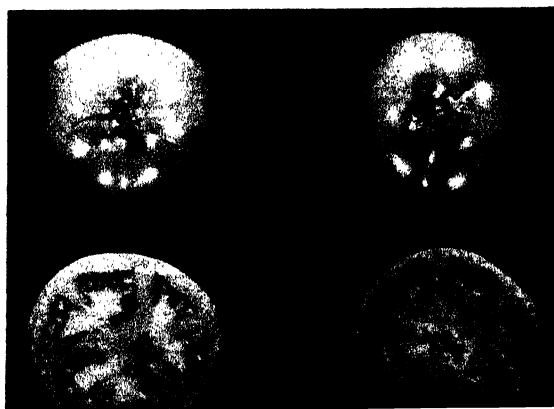
the samples taken from various levels within the bottle will show a graduation of cream concentration. It has been established that certain growth-controlling substances, similar to hormones, are produced within the plant and diffuse from their point of origin in the meristem to other parts of the plant. Such growth substances, termed *auxins*, appear to play a major role in the increase in length of cells, and thus in the differentiation of special tissue. Auxins have a differential effect on different types of tissues. One which will stimulate growth in a stem will in a similar concentration inhibit growth in a root. It can be shown that the meristem is the source of the auxin, for if the tip of a young growing plant is removed, it will no longer respond to light or grow into the earth, whereas if the severed tip is replaced, the original tropic reaction is restored. Even a piece of gelatin which has been in contact with the growing tip will have the power of restoring tropic reaction in the stump of a decapitated shoot if brought into contact with it. This indicates that a chemical substance, the auxin, first diffused into the gelatin and from it into the stump (Fig. 177).

Many of the tropic reactions of a plant are due to growth influenced by auxins. Thus if the proper concentration of an auxin acts on one side of a stem, that side will elongate faster and cause the shoot to bend away from the

point where the auxin was applied. Since the same concentration of auxin has the opposite effect of retarding growth, in a root, a root so treated will grow toward the side stimulated. By gravity, auxins appear to concentrate on the lower sides of plant structures. So if a plant is placed horizontally, its shoot will grow upward and its root downward. Auxins also accumulate in greater concentration in tissues that receive less light, and thus produce the typical positive and negative phototropic reactions of roots and shoots.

The development of fruit is also controlled by auxins produced by the developing seed, and unfertilized blossoms generally fail to produce fruit. Auxins or plant hormones are being put to increasing commercial use. The application of certain ones to blossoms causes fruit development without the stimulus of seeds inside, making possible the production of seedless fruit (Fig. 178). Similarly, auxins, both natural and synthetic, can be used to stimulate root formation in cuttings for plant propagation. Other hormones can prevent premature dropping of apples. A commercial hormone, 2-4D, used for weed-killing, performs its action by inducing abnormal and distorted growth and consequent unbalance and death in the plant. Others may prolong dormancy (so being useful in potato storage), while still others shorten dormancy periods and make it possible to force flowers to bloom out of season. The possibilities inherent in the increased knowledge of auxins as applied to these fields seem almost unlimited.

Fig. 178. Seedless tomato at right was produced by treatment with synthetic growth substance. Compare normally pollinated tomato at left.



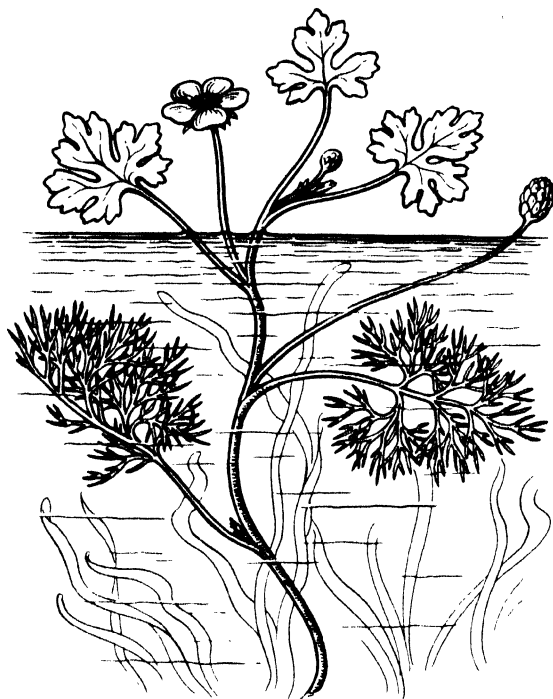


Fig. 179. In the water buttercup, submerged leaves contrast sharply with those growing in air.

Environmental Stimuli. Environmental conditions also play a role in determining the nature of cells produced from undifferentiated meristem tissue. Variations in light, temperature, water, and other factors may have profound effects on the appearance and behavior of a plant (Fig. 179). Witness the difference in the size and structure of leaves grown in the shade as contrasted with those on the same plant that have grown in the sun. Etiolation (Fig. 180), the peculiar effect of an absence of light on plant structures seen in the pale enormously elongated shoots of stored potatoes kept in the dark, or in similar shoots of other plants growing under buildings, is another effect of auxin. Here, if darkness is not too prolonged, the response appears to be useful, for it enables the plant to grow more rapidly in length, though at the cost of strength and balanced structure. This may give it a chance to reach the light, without which it would eventually die.

The shape and organization of a normal plant are just as clear evidences of response and coordinated growth as are the experiments which show reactions under abnormal conditions. The growth of a leaf is obviously not merely a matter of cell proliferation. This alone would result only in an undifferentiated spherical mass of cells. The delicately adjusted production of growth substances in cooperation with environmental stimuli produces the functionally perfect pattern of the leaf, and also determines its position on the tree.

Thus the embryonic development of a plant is never finished. Throughout its life, the embryonic tissue, the meristem, proliferates, producing more meristem as well as other cells that are shaped into the mature tissue of the plant under the influence of the growth substances, the auxins, working in coordination with the environmental stimuli. It is thus that the wonderfully coordinated plant body is achieved. We may now examine the detailed structure of this body.

Fig. 180. Absence of light affects growing turnip shoot which is unusually long and pale yellow. This effect is known as etiolation.



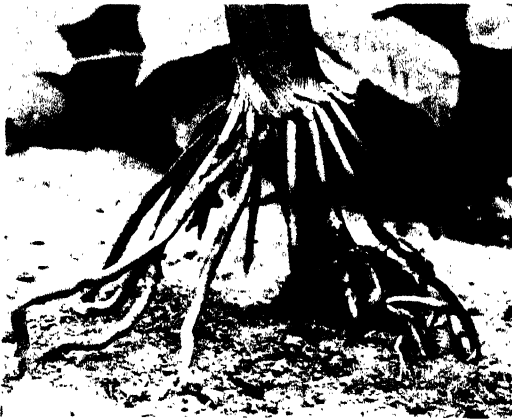


Fig. 181. This corn plant illustrates the dominant role played by adventitious roots in some plants.

The Roots

When we think of a plant, we usually think of the parts we can see, although, like an iceberg, well over half of the plant may be invisible. While roots vary in form as much as does foliage, they are of two main kinds, *primary* and *adventitious*. The former consists of the taproot, the first root of the seedling, which continues to grow and may dominate the entire root system, together with its secondary branches, which may spread in all directions to produce a fibrous mass. The latter are roots which arise above the original root, usually from the stem, and may eventually become quite extensive (Fig. 181). They may also arise from stems obviously not destined to produce roots under normal conditions, as in the preparation of cuttings for plant propagation.

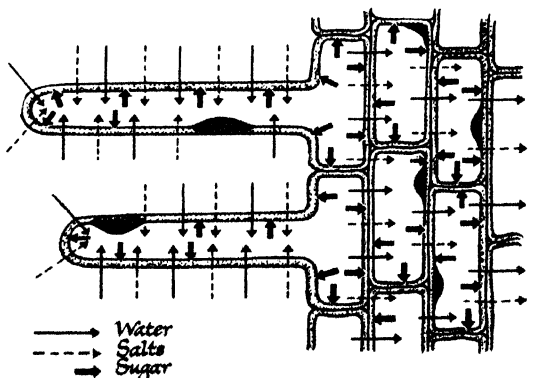
One of the most extensive root systems investigated is that of the bush morning glory, *Ipomoea leptophylla*. This sand-hill dweller has been found to possess a root system that may cover a radius of twenty-five feet and extend to a depth of ten feet, although the visible plant measures only about thirty inches high and has a diameter of but two feet. The root system occupies a volume of soil of about 10,000 cubic feet, contrasted with a shoot volume of only about four cubic feet, so that the ratio between the two is about 1 : 2500. Only

the tips of the roots, where the root hairs grow, are constructed for absorption and actively engage in it. During the life of the plant these tips are constantly on the march during the active season, and the plant is constantly migrating to new soil areas.

Since many plants spread in similar fashion, artificial plant food given to large plants such as trees should be placed at a distance from the trunk corresponding to the size of the tree. Usually most of the feeding roots are at approximately the same distance from the trunk as are the tips of the branches. For a similar reason irrigation, to be beneficial, should be at widely separated intervals and should be thorough. In this way the moisture encourages growth of roots to deeper soil layers, where it can be retained for longer periods. Superficial irrigation, on the other hand, causes roots to restrict their development to superficial layers of soil, with the result that a major portion of the root system will die if that thin layer dries out.

The Root Hairs. The temporary delicate root hairs enormously increase and extend the contact between the plant and the soil (Fig. 182). The tissue of the root hair comes into intimate contact with the individual soil particles, and thus with the films of moisture and dissolved materials that surround them. Root hairs average about .01 mm. in diameter and may extend up to several millimeters in length. The surface of each hair exceeds that of the base upon which it stands by about 200 times. Actually, only some 10 per cent of the root surface

Fig. 182. Movement of dissolved substances into and out of a root is greatly increased by absorptive surface of root hairs.



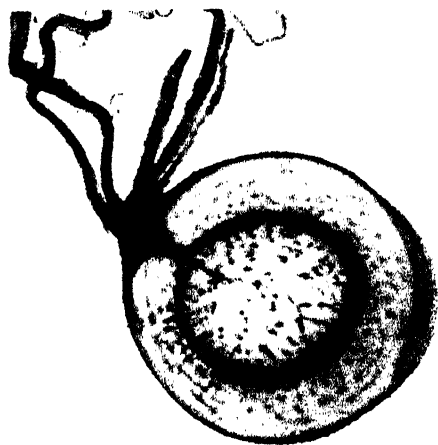


Fig. 183. Cross-section of root showing concentric cylinders and origin of lateral root.

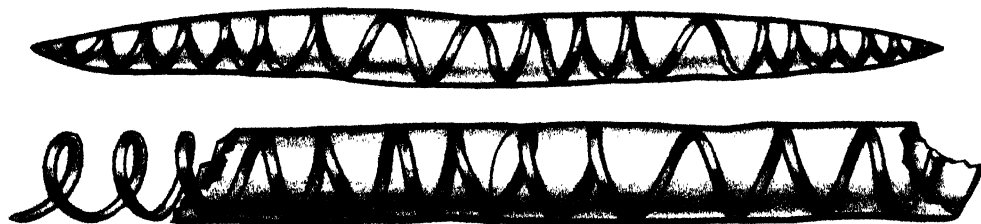
supports root hairs; even so, the increase in absorbing surface so attained is vital. The effect is enhanced even further by the greatly increased volume of soil reached, and by the intimate contact between soil and root hairs.

Soluble substances diffuse through water which touches the root hairs, seep with it through the cell wall, and then diffuse through the cell membrane. Water, too, enters the cell by osmosis. Further diffusion through the cytoplasm and the sap vacuole within the cell brings these substances to internal cells where the processes are repeated until the absorbed materials reach the vascular tissue. Smaller inorganic molecules in the water, as well as molecules of the water itself, pass through cell membranes with relative ease, while the larger organic molecules, such as sugars and proteins within the plant, are unable to pass out in the opposite direction.

Clearly, undisturbed activity in the root is vital. Any marked disturbance, chemical or physical, is likely to be harmful to the plant. It is because of the delicate nature of the root hairs, which make up the largest portion of the absorptive system, that transplanting is such a severe shock to many plants. Unless a solid ball of earth be moved with the root, most of the root hairs will be crushed or torn, and the plant will suffer through lack of moisture until growth can restore the absorbing surface. If the roots are unavoidably torn, it will be helpful to reduce the loss of moisture by keeping the plant in the shade, watering it copiously, and decreasing evaporation by removing some of its foliage.

The Root Tissues. We have already said that the root consists of the same three concentric cylinders as the stem, the vascular stele, surrounded by the cortical system, and the epidermal layer (Fig. 182) which produces the root hairs. The outermost layer of the stele consists of cubical cells from which the secondary or lateral roots arise. These must force their way through the cortical tissue and through the epidermal layer (Fig. 183). Conspicuous in a young root is a cross-shaped structure within the stele, formed by the tubes called *tracheids* (Fig. 184). These are the main structural parts of the water-conducting system, the xylem, through which water constantly mounts from the roots to the aerial parts of the plant. Between the rays constituting these ducts are the sieve tubes of the phloem with their companion cells, making up the system for conducting organic foods. As the root matures, a cambium layer appears just outside the xylem and inside the phloem. It eventually forms a complete ring, gradually spreading both inward and outward. With these structures, the plan of the mature root is established.

Fig. 184. Tracheid and duct with spirally thickened walls.



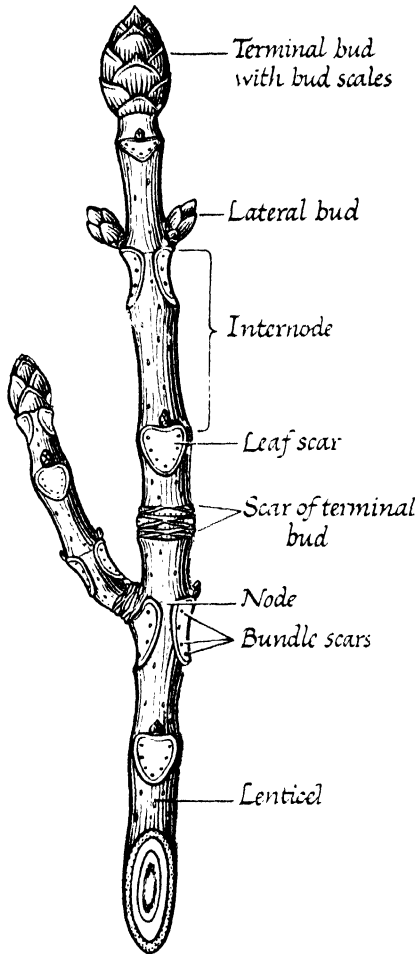


Fig. 185. Woody twig of a horse chestnut in winter condition.

The Stem

The stems of vascular plants range from the slender herbaceous stalks of the grasses, which die back to the ground each year, to the woody trunks of the giant sequoia or redwood trees, which endure for centuries. But whatever its size or the length of its life, the stem serves the same basic functions. It is the intermediary between roots and leaves. Through it run the tubes and ducts; it is a place of storage for food reserves; and it holds the leaves high enough above ground so that they may carry on photosynthesis. Herbaceous plants and shrubs may produce leaves on all parts of their

branched stems throughout their life, but in woody plants, especially trees, the leaves generally grow only on the more terminal regions. The stem grows in length only at its terminal points, so that a nail driven into a tree three feet above ground will still be three feet above ground ten or twenty years later, though it may by then lie deeply buried in the thickened trunk.

Growth of the Shoot. Growth in length may be easily understood by examining a young twig of a tree such as a horse-chestnut. The base of the twig shown in Figure 185 is two years old. The region between the "scar of terminal bud" and the tip of the branch is one year old and was produced during the growth period of the previous summer. In the spring preceding the winter condition shown, a terminal bud, like the one shown at the end of the twig, occupied the position of this scar. When warm weather arrived in the early spring, the meristem within the terminal bud resumed its activities and began to produce new cells. The modified leaves, or bud scales, dropped off, leaving their scars. A leaf was produced at the point labeled "leaf scar," and the broken ends of the fibrovascular bundles that once extended into the leaf are visible. Lateral buds were also produced, some of which, due to auxin distribution, are stimulated to grow in the following season to produce branches, while others will remain dormant. Many such dormant buds are reserves and may never develop unless the terminal bud is injured or removed. At the close of the season, the meristem had produced another terminal bud, actually a miniature branch with tiny leaves all wrapped and protected within the outer modified leaves, the bud scales. In this condition the stem lay dormant through the winter, after its leaves dropped at preformed points under the influence of plant hormones. Thus no matter how old the tree is, its terminal branch tips are never more than a year old.

Branch and Fruit Formation. The pattern of branch and fruit formation could be seen in the twig of an apple tree in its third year of growth. The terminal portion would of course be growth

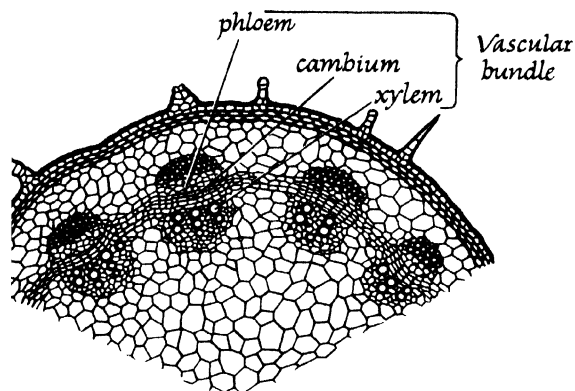


Fig. 186. Cross-section of sunflower stem showing continuous cylinder of cambium with fibrovascular bundles.

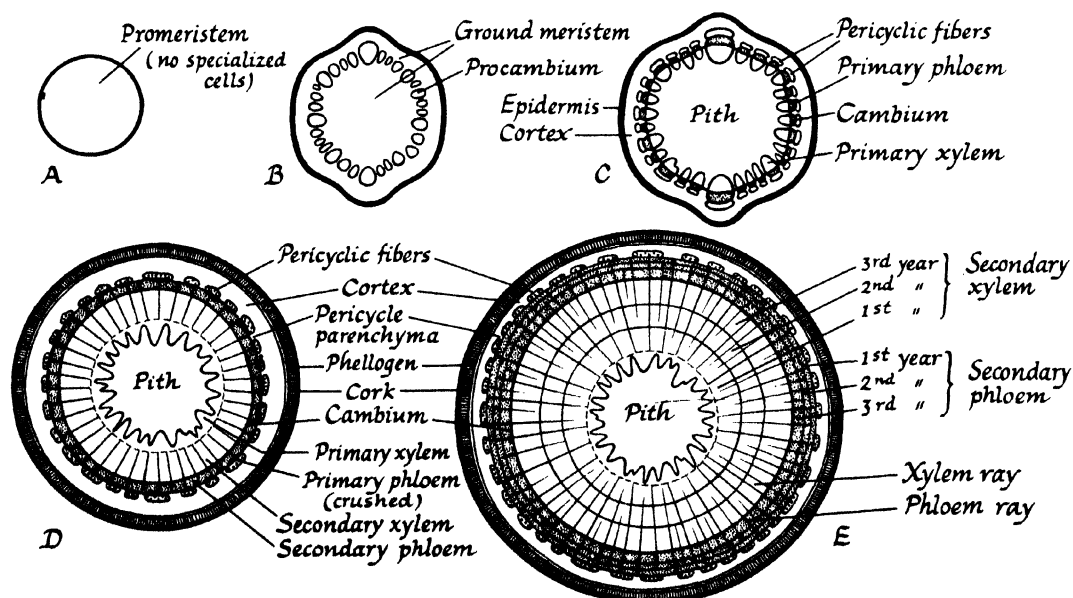
of the current season. At the base of this portion are bud scars, left when the bud scales dropped off the previous spring. In the segment below this would be lateral buds, or young spurs. That these are not to become leafy shoots would be indicated by retarded growth. Some of the lateral buds would show even more retardation than the young spurs. They are the latent buds. In the segment below this one could see that the young spurs of the previous season had become fruiting spurs. Whether

a bud will become a flower bud or a branch bud is determined during the period of bud formation, by metabolic conditions the nature of which is unknown. The points of attachment of the blossoms or fruit are visible as stumpy scars. These spurs will repeat their action of the previous season in the following one, some producing blossoms and others making merely limited vegetative growth. Usually a fruiting spur will blossom in alternate years. Should the blossom buds be destroyed by frost in one year, they may respond by fruiting the following year, together with those that would have fruited anyway. In this manner an annually bearing tree may develop a biennial habit.

Stem Tissues

The internal structure of the stem shows practically the same tissues as the root, though with some changes in pattern. The basic structure of a woody stem may be understood by studying the structure of a short-lived herbaceous stem, such as the sunflower (Fig. 186); for an herbaceous stem, except that it has less xylem tissue, is very much like a young woody stem. In the cross-section of the herbaceous

Fig. 187. Cross-sections of stem of elder (*Sambucus nigra*). *A*. Stem in young bud. *B*. Differentiating stem. *C*. Young stem beginning cambium formation. *D*. Stem in first year of growth, showing secondary xylem and phloem. *E*. Stem three years old.



stem the main features are (1) the central pith, (2) the cortex, in which separate fibrovascular bundles are arranged in a circle near the outer perimeter of the stem, and (3) the circularly disposed cambium that cuts through the center of each vascular bundle. Minor features are the cortex and the vascular bundles which strengthen the stem mechanically.

There is a similar disposal of tissues in the young stem of the elder, *Sambucus* (Fig. 187). Its subsequent growth from year to year clearly shows how the solid wood of the trunk is derived from the fibrovascular bundles in a ring of columns disposed upon a cambium cylinder (Fig. 187-D, E), which is gradually pushed away from the center of the stem by the wood it has produced. New fibrovascular bundles become interspersed between the original ones, and finally merge to form a continuous cylinder located between an internal column of wood and an external sheath of bark. Early in this development, the epidermis, cut off from its supply of food by the tissue growing under it, dies off and disappears. The cells of the cortex tissue beneath it develop thick walls and form the dead outer bark of the tree. This may flake off in various patterns or build up to an appreciable thickness, as in the cork oak. The manner in which it flakes off gives the tree its characteristic bark pattern.

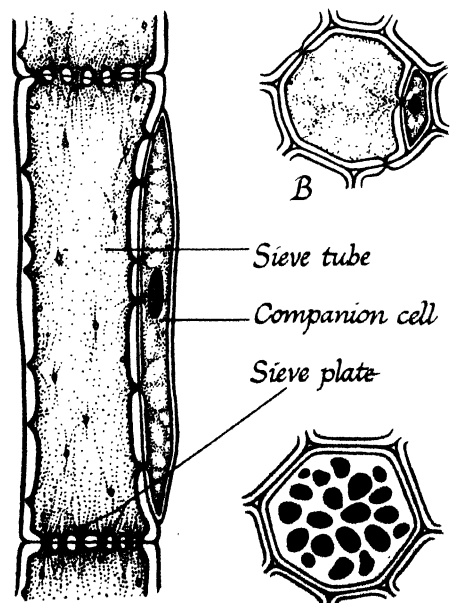
The Cambium. The growth of the cambium is not a steady process in dicotyledonous plants, but is influenced by the seasons. The ducts formed in spring are larger and have thinner walls than those formed in summer. Hence, instead of being uniform, the wood develops concentric circles or rings of softer spring growth and harder, more compact summer growth. Each ring of dense wood thus denotes one year of growth. So the tree carries within its trunk a record of its age, as well as of the growing conditions during each year of its life. Favorable conditions of course bring rapid growth, while trees growing on poor soil or under severe climatic conditions, as on mountain tops, grow very little from year to year, and may remain quite small even at a venerable age. It has been possible to make charts

of the climate of past ages based on the rates of growth shown in the trunks of trees. Since climatic sequence is unique for any particular region, all trees of that region show the same growth sequence in their annual rings. It has even been possible to date prehistoric dwellings by comparing the annual rings of logs used in their construction with the annual rings of living ancient trees.

The Xylem. The cells produced in the xylem by the activity of the cambium become either parts of the ducts or wood fibers. The most primitive type of wood cell is elongated and pointed at both ends. Overlapping, these cells form the mature conductive tissue in simpler plants and the earlier stage of such tissue in higher plants. The walls of these become thickened and lignified (woody). In some, lignification almost fills the inner space of the cells, and the dead cell wall becomes a wood fiber. In others, which become parts of ducts, only the walls are lignified.

In addition to these vertical conducting tissues, there are horizontal ones, which constitute the medullary rays of wood. These are

Fig. 188. Sieve tube and companion cell in phloem of herbaceous plant stem. A. Note protoplasmic continuity through the perforated end walls of tube cells. B. Section through sieve tube and companion cell near nucleus of the latter. C. Sieve plate.



fine radial lines, consisting of thin-walled ray cells, sometimes associated with tracheids. Such rays may begin in the pith and radiate through the wood, or they may originate at any point in the wood and radiate outward. Their function is lateral transportation.

The Phloem. The portion of the fibrovascular bundle on the outside of the cambium is the phloem, with its characteristic sieve tubes, their companion cells, and the phloem fibers (Fig. 188). Parenchymal cells and medullary rays may extend into the phloem. In older stems, like tree trunks, the cork and cortex layers are quite thin compared to the trunk, so that removal of a relatively thin layer of bark will penetrate to the cambium. Serious damage may thus be inflicted on a tree, for the removal of bark to the cambium also removes the phloem with its sieve tubes, and so interrupts the transport of sugar solutions from the leaves to dependent tissues such as roots. Lacking sugar, the roots die, thus robbing the plant of its ability to absorb water, and swift death of the entire plant follows. If a tree is girdled, that is, if a strip of bark is removed around the entire trunk, it will not die at once, for the roots have some food reserves, depending on the season of the year, and so they may continue to function for months, during which time the leaves still receive ample supplies of water and dissolved salt. Eventually, however, the roots die by starvation, and this is followed by rapid wilting and death. From the standpoint of selection and survival, it is astonishing that such vulnerability should have persisted in these otherwise highly adapted organisms. For many trees, both young and old, are killed through girdling by deer, mice, and other animals.

Trees which have been girdled may be saved by *bridge-grafting*, a common process which throws some light on the growth and regenerative capacities of trees. Since death by girdling is caused by severing the tubes of the phloem, a piece of bark grafted to the bark on both edges of the break would save a tree. The simplest way to achieve this is by arching across the gap pencil-thick twigs cut from the

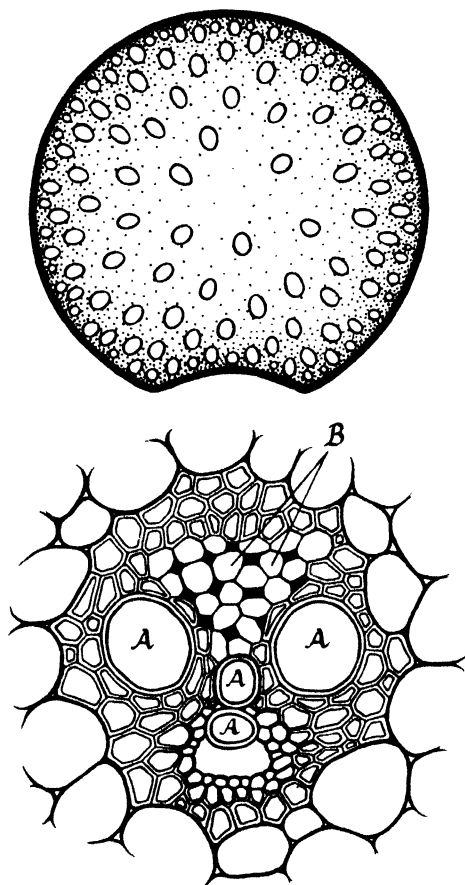


Fig. 189. Above: Stem of monocotyledonous plant in cross-section. Fibrovascular bundles are scattered through the pith. Below: One of the bundles magnified. A. Vessels. B. Sieve tubes with companion cells. The bundle is surrounded by a sheath of thick-walled cells.

same type of tree. If this is done so that the cambium layer of the twig meets that of the tree, regenerative processes in both will result in a rearrangement of the sieve tubes, so that a continuous conducting system is once more established before the food reserves of the roots have become exhausted. The twigs will increase in thickness from year to year, as a result of their own cambium activity, and will eventually form a continuous layer of bark around the trunk.

Monocotyledonous plants, such as grasses and lilies, develop fibrovascular bundles basically similar to those in dicotyledonous plants.

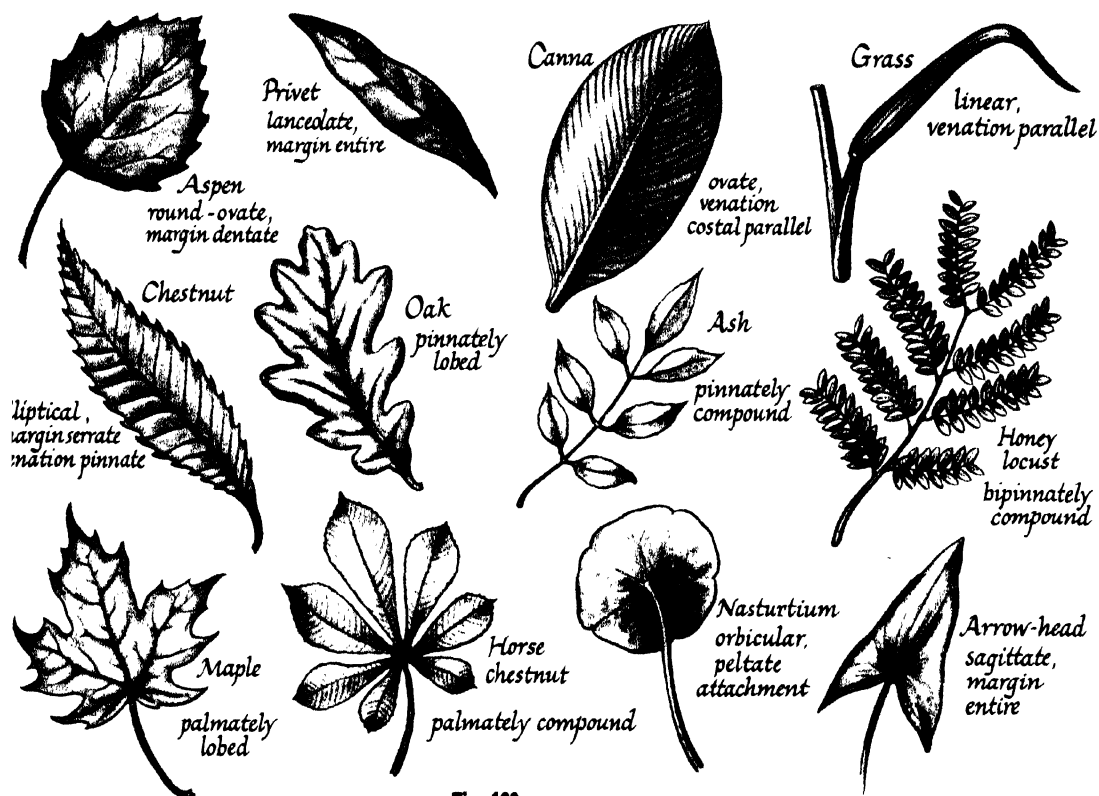


Fig. 190. Some types of leaves.

There is, however, no distinction in monocots between pith and cortex, and no cambium layer separates the two regions. The fibrovascular bundles, instead of being arranged in a cylinder, are irregularly scattered throughout the stem (Fig. 189). The arrangement of the xylem and phloem in the bundles, traces of cambium in some monocotyledonous plants, and certain other features indicate that the monocotyledonous stem has evolved from dicotyledonous types.

Why Water Rises in Plants

There is still considerable uncertainty about the forces responsible for pumping the soil water up from the roots through the entire plant. The work thus achieved is often considerable. For instance, it would take a hundred pounds of pressure to push water to the top of a two hundred foot tree. Known forces that cooperate in this process are osmotic pressure, capillarity, and atmospheric pressure.

There is no doubt that osmosis plays a major role in the passage of water from the soil into the roots. But it is not fully clear what part osmotic pressure plays in transmitting the water from the root cells to the ducts. The ducts have no living tissue and are filled primarily with a watery solution like that in the soil already, while the root cells, containing protoplasm, represent a solution of higher concentration — that is, they have higher osmotic pressure. Hence water should not flow from the root cells to the ducts, but in the opposite direction. It is probable that a secretory action by the root cells actively transmits water into the ducts as a result of some sort of work in the cells not well understood. Once the water is in the ducts, capillarity would account for an appreciable part of the force that causes it to rise. Atmospheric pressure could account for a straight rise of twenty feet or more. This principle is generally, but not very accurately, referred to as suction or traction. It may be

visualized briefly as follows: as water is evaporated from the leaves, pressure within the ducts drops to a point below that of the atmosphere. Cohesion of the water molecules within the ducts transmits this drop in pressure along the line, and the excess pressure below results in a rise of the entire column of water. Thus transpiration assists in the rise of water in a stem. Finally, the roots themselves perform a kind of pumping action, which can be seen in the fact that the stumps of plants whose upper parts have been cut off continue to exude moisture for some time. This, at least, is the present theory.

Leaves

The leaves of plants are of the most varied sizes and shapes, from the minute scale-like leaves of a sequoia to the giant leaves of a banana plant, and from slender, thread-like processes to great sheets (Fig. 190). The primary function of the leaf is photosynthesis, yet some leaves have become adapted to completely different roles. Thus in some peas certain leaves have become tendrils which aid the plant in climbing. In the barberry some leaves have become spines. In certain plants,

like the parasitic dodder, the leaves have been reduced to functionless scales. Others, like the cactus, have leaves only in their seedling stages, while in the mature plant the stem takes over the function of photosynthesis (Fig. 191).

Yet the importance of leaves in the life of most plants can hardly be overstated. It has been estimated that a medium-sized elm may have as many as seven million leaves with a surface area of about five acres. Such a tree may lose seven tons of water through its leaves in twelve hours of a clear dry day. A square meter of leaf may produce between 0.5 to 1 gram of carbohydrate per hour. Thus the medium-sized elm should be able to produce twenty to forty pounds of carbohydrate per hour under favorable conditions. An acre of corn may produce the equivalent of two tons of sugar per year, about one quarter being stored in the grain and so available as food for man and animals. These are of course only approximate figures, and values vary considerably for different plants, seasons, and soils.

Leaf Structure. The typical leaf has a broad, flat blade, attached to the stem by a stalk called the *petiole*. In conifers, however, the leaves are often more or less cylindrical or

Fig. 191. Modifications of leaves. *A.* Leaf of tulip tree, with well developed stipules at base of long petiole. *B.* Garden pea. The large stipules are important in photosynthesis. Leaves at ends partially transformed into tendrils. *C.* In the barberry, the leaf has become a spine, while the axillary bud has produced a cluster of four leaves.



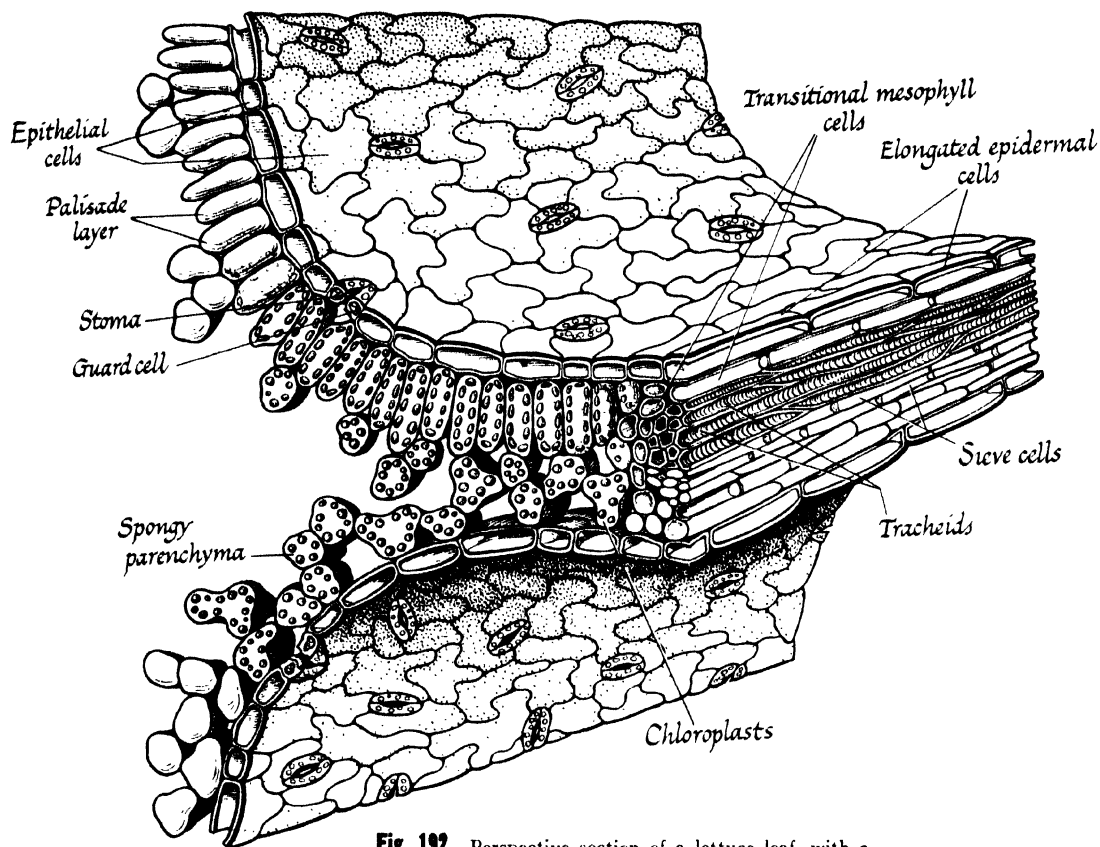


Fig. 192. Perspective section of a lettuce leaf, with a fibrovascular bundle cut transversally and longitudinally.

needle-shaped, and may endure for several years instead of being discarded annually as in most of the more advanced angiosperms of colder zones. Despite their shape, the structure of these needles is much like that of the leaves described here. A flat leaf is a more efficient light absorber, but it is clear that it is more vulnerable to winter damage. Thus most flat-leaved plants of temperate zones are deciduous. Within the blade of the leaf, the fibrovascular bundles leading from the petiole form a midrib, which in dicotyledonous plants branches out in the familiar manner to form veins. Within the relatively waterproof outer layers are the thin-walled and generally loosely arranged chlorophyll-bearing cells. Breathing pores, the *stomata*, facilitate gas exchange.

It is possible to learn a good deal about the fundamental structures of the leaf simply by slicing, peeling, and crushing a living lettuce

leaf and observing the fragments under the microscope. The surface of the leaf is seen to consist of an exceedingly thin tissue of flattened, irregularly shaped cells that interlock much like the pieces of a jigsaw puzzle. These are the *epidermal cells* (Fig. 192). The outer surface of these cells is relatively thick and colorless, and they have no visible internal structure. Scattered here and there over the surface are striking oval structures, which consist of two sausage-shaped cells with their concave surfaces facing each other, leaving a small elliptical opening between them. These twin-celled structures are guard cells, and the openings between them are the *stomata*, breathing pores through which moisture escapes from the leaf tissue and carbon dioxide and oxygen are exchanged in photosynthesis. The magnitude of the gas exchange through the stomata is indicated by the fact that in one hour a leaf

requires an amount of carbon dioxide equivalent to that in a six-foot column of air standing upon its surface. Multiply this by the number of leaves on a tree, and the figure becomes truly impressive.

The stomata are more than simple pores, for the guard cells that border them regulate the size of the opening. When the water supply is ample, these become turgid, or swollen, through osmosis, and because of their curved shape, their center portions move away from each other, leaving a clear opening, the stoma. If the water supply fails, the guard cells tend to collapse, thus more or less effectively sealing the opening. When this occurs, transpiration is reduced, but so is the exchange of carbon dioxide and oxygen, so that photosynthesis too is curtailed or even stopped.

The number of stomata on the surface of a leaf may range from 200 to over 100,000 per sq. cm. The number varies with the type of plant, but it may also vary on different leaves of the same plant, depending upon whether the leaf gets much or little sun, or whether the plant is growing in dry or moist soil. Plants growing on dry soil have fewer stomata. Most plants have fewer stomata on the upper sides of their leaves than on the lower, and many, such as most deciduous trees and shrubs, have none at all on the upper side. This is adaptive, because in plants growing in dusty or dry places, the upper stomata become clogged by dust particles and are thus at a disadvantage.

The Parenchyma. Beneath the epidermal layer of the leaf there is a spongy mass, the parenchyma, composed of thin-walled, more or less spherical cells with numerous small, rounded or flattened chloroplasts hugging their inner surfaces. In many plants the upper layer of these green cells differs from the lower. In the lettuce leaf the difference is noticeable, though not pronounced. The upper, or *palisade*, layer usually consists of somewhat elongated cells, closely packed and standing on end. The greatest photosynthetic activity is thought to occur in these cells. Lying beneath the palisade layer is the *spongy parenchyma*, a characteristic feature of which is its loose arrange-

ment. This greatly increases the amount of cell surface in contact with air, sometimes by as much as twenty times the surface area of the leaf.

Vascular Tissue. Running through the parenchyma are branches of the fibrovascular bundles of the stem. The delicate structure of the lettuce leaf makes it easy to see the fine details of this structure. These "veins" resemble bundles of glass pipes, each with one or two plastic rods wound helically around its inner surface. These pipes are the spiral ducts, the only type of duct in the leaf. These woody ducts have the same function as elsewhere in the plant; that is, they conduct water and mineral nutrients. Running parallel with the ducts are elongated cells with thickened walls, though in the lettuce leaf these are only slightly thickened. These provide mechanical reinforcement and support the leaf blade. Most of the elongated cells surrounding the ducts, thin-walled and not highly differentiated, appear to act as intermediaries. The trend toward elongation in these conducting tissues is visible even in the epidermal cells above and below the vascular bundles, for here the epidermal cells lose their typical scalloped effect and become straight-walled and long. As in both stem and root, sieve tubes accompany the ducts and conduct synthesized food from the leaves down the petiole into the stem and perhaps ultimately to the root.

Arrangement of Leaves. Since it is the function of the typical leaf to absorb sunlight, we should expect to find special provisions in the plant to favor it in its work. Even casual observation shows a marked tendency for leaves to be arranged so that they do not seriously interfere with each other's access to the light. Thus in some plants, like the common dandelion and plantain, the leaves are arranged radially around a short stem. In many others, terminal leaves have short petioles and those farther down the branch have longer ones, assuring maximum exposure to light for every leaf. Most plants grow so that the face of the leaf is at right angles to the incidence of the sunlight. This may be strikingly observed by

looking up into the foliage of a catalpa, or almost any other tree, from a few feet away and then again while standing at the base of the trunk. In the first case it is possible to look through the foliage so that the trunk and the branches are visible, for the leaves are largely oriented edgewise to the viewer. In the second case the leaves block out almost the entire sky, indicating that almost every ray of light that strikes the area of the tree strikes a leaf and may be absorbed.

Special Movement of Leaves. Most of the response movements of plants are due to local variations in rate of growth, such as the tropisms previously mentioned. But plants are capable of other movements also. The photonastic drooping or "sleep" movements of certain leaves, which occur during the night, are of this kind. Striking are the relatively rapid movements of special structures in such highly specialized plants as the Venus' flytrap (*Dionaea*), the sundew (*Drosera*), another insect catcher, and especially in the astonishing sensitive plant *Mimosa pudica*. Like the sleep movements of leaves and unlike most tropisms, these movements are reversible and are caused by changes in the turgidity or osmotic pressure of certain cells at hinge points or points of movement. A slight jar or shock causes the mimosa to fold its leaflets (Fig. 193). The response is not localized within the part stimulated, but is progressively conducted to adjacent regions. Thus a strictly localized stimulus, such as the heat of a match-flame held near a single leaflet, causes the leaflets to fold up pair by pair down the whole length of the leaf. Startling as this is, it is still more astonishing to see the leaflets on an adjoining leaf next experience the same reaction, folding up by twos, but this time from the base of the leaf towards the apex. This may continue from leaf to leaf, whereupon each entire leaf will bend at the point where the petiole joins the stalk and collapse like a folded umbrella. The mechanism of this amazing response has been the subject of considerable research, but it is not yet fully understood. It appears that a hormone is produced and transmitted with re-

markable speed through the vascular system. Both xylem and phloem appear to serve as paths of propagation. Nothing in the plant world offers a more startling spectacle than the simultaneous collapse of a bed of these plants when struck by a sudden gust of wind. The functional value of this reaction is somewhat problematical, though movement in the insect-catchers helps the plants to survive. The leaf is the most efficient photosynthetic organ among plants today. That does not mean, of course, that evolution may not some day produce an even more efficient leaf. It would be curious indeed if it did not.

PLANTS, SOIL, AND MAN

Living organisms often give the illusion of being self-contained units, and we are too apt to study them as such. But if we do this and no more, we have really ignored half the story. In a very real sense, every organism is a subordinate part of a complex, interacting living unit which includes all the plants and animals in its immediate environment. Each is in contact with others, either directly as hunter and hunted, as eater and eaten, as symbiotic partner or parasite, or indirectly through the medium of the products the others remove from and leave in the common media of soil, air, and water. Each organism, no matter how insignificant, causes changes in the medium surrounding it, and these changes in turn influence the form and behavior of other organisms within the common medium. Such interrelationships are of extraordinary complexity and are still but imperfectly understood, but we can say with confidence that not a single bacterium can be removed from the soil without tipping the balance of the immediate community either in one direction or another. We have come to realize that any community of organisms, just like any individual organism, is a dynamically balanced structure, changing from minute to minute, and thus in no two consecutive minutes the same. It is one of the great marvels of nature that such delicate balance has evolved into a self-adjusting sys-



Fig. 193. The sensitive plant; with leaves folded (right) at the touch of a pencil.

tem that produces a stability through equilibrium which may endure for centuries or even millennia. And it is not too difficult to see how this must have come about. Any organism not so adjusted would so upset the balance as to destroy the entire cycle. The result must of necessity either be an effective balance, or no balance at all, and hence no life at all.

Soil, water, and air are the media in which such balanced units must exist, and it is not pure accident that the gas exchange of animals and plants is such that one exactly balances the other, or that other metabolic processes of these fit one into the other like the wheels of a finely made machine. Countless millions of years of selection have permitted only those to live which were so fitted, and for each organism that passed the screening of selection, thousands failed and were eliminated, frequently carrying with them scores of organisms that might otherwise have passed the test.

A medium of the greatest importance in such relationships is the soil. To the undiscerning, soil is just so much inert earth. Examined closely, however, it is seen to be a complex dynamic system of water, solutes, colloids, coarse and suspended particles, both organic and inorganic, and many different forms of living organisms. These are all intrinsic parts of the soil, and thus soil is in fact a living system in much the same sense that the reader of this book is a living system. Soil is a product of living organisms and is itself dynamically

alive. It can no more be placed in a jar and set aside as a sample than can any other living organism. It is in this complex living medium that most plants live, and it is upon this inter-relationship that virtually all other living organisms depend.

Just as there are many kinds of organisms, there are also many kinds of soil, depending on the amount of rainfall, average temperature, the nature of the inorganic sand and clay particles which make up the bulk of its weight, and many other factors. And the nature of the soil determines the kind of vegetation that grows upon it, which in turn determines the nature of the other organisms that depend on the bounty of the plants. Soil, then, is an aggregate of minute sand and clay particles, many of them colloidal in size, interspersed with miscellaneous fragments of organic matter in various stages of disintegration and held together in the form of loose flocculent crumbs by the adhesive and cohesive property of water. Also, the water contains varying amounts of dissolved mineral matter and gases absorbed from the air which diffuse through the pores of the mass.

Soil capable of supporting flourishing plant growth must have a proper chemical balance as well as the prescribed physical structure, and only plant growth can maintain in the soil conditions for continued plant growth. The chemical activity of burrowing roots, aided by bacterial action and by other soil organisms, and the contribution of organic plant tissue are

necessary for the maintenance of healthy soil. Soil which has become denuded through some agency such as fire or the axe and plow of man, is a system badly off balance. For a while, bacteria and fungi continue their saprophytic activities in breaking down organic compounds still present, thus liberating plant foods but reducing the percentage of organic compounds. But soil particles lose their flocculent nature and break down into their minute component sand or clay particles, thus assuming a more compacted condition within the mass which greatly reduces air and moisture spaces. Finally the soil becomes dead: it no longer acts and breathes and may assume the sterile condition of stone. Its absorbent nature is lost, too, for its capillarity has depended on the great total surface of the floccules which were maintained by its organic components. No longer crumbly, the surface becomes impervious, and the inorganic particles form a layer of dust upon the hard cracked mass, to be whirled away by the wind or washed into streams, leaving only coarse sand and pebbles behind.

But the disruption goes much farther than this, for soil for many miles around such dying areas may in turn become starved and sick as a result. A vicious cycle has set in, a cancer of the soil which can destroy in a few years a biological system which was tens of thousands of years in building. Fewer plants mean poorer soil and poorer soil means fewer plants; — thus forests and grasslands may become deserts. For healthy porous soil acts like a sponge. Rain does not fall upon it, but upon the protecting plant cover, to seep gently into the porous mass. Capillarity holds it there long after the rainfall has stopped, and doles it out to the delicate absorbent root hairs of the plant cover, permitting only a slow steady seepage to the drainage basin. Much of the essential soluble mineral matter freed by root action and bacterial action is held where it is available to plants instead of leaching away. Rivers flow clear, and the landscape endures, for the plant organisms upon the soil and in it successfully cooperate in softening the violence of climatic conditions, so perpetuating conditions favorable for continued

plant growth and the animal life it must needs support. So successfully have plants been selected in their constant struggle and competition with animal life that with their tough bark and exuberant growth they are normally scarcely checked by the modest tribute exacted. Primitive man, like other animal life, found his niche in this cycle, but with the dawn of human culture the scene changed.

Man discovered fire. Natural fires probably showed him the way, and demonstrated too that immediate results of brush or forest fires could contribute toward a temporary easing of his problems in the everlasting search for food. After a fire, game was exposed or possibly killed and trapped. He could not know that lowered production and scarcity would follow on the heels of this plenty. And if it did, there was nothing to hinder him from moving elsewhere. He could not know that the denuded ground was altered perhaps for decades to come, and that he had killed not only the visible vegetation above the ground, but some of the invisible life beneath the soil upon which the plants grow. The cycle was broken, but only temporarily, and only in patches. Blasted areas left to themselves could build up again in the unmolested decades to follow.

But man's powers increased. He discovered how to make tools, and he discovered how to grow plants for food and how to breed and care for animals. His rate of multiplication, previously held in check by the hazards of a hunter's life and the uncertainty of food supply, now increased greatly under the new opulence brought about by his new skills. Great herds of cattle grazed the grasslands, and fire became an ally of man in eradicating unproductive forests to produce still more range and arable soil. The earth was first scratched and then violently torn by his new instruments, especially by the plow powered by his draft animals. The delicate biological balance that had endured for millions of years was disturbed, and organic matter was used up faster than it could be replaced; for in order to produce plentifully, planted crops had to be spared competition with wild plants, the soil had to be cultivated

and denuded. Soil temperatures rose in the unprotected fields, bacterial action increased, and the decomposition of organic matter was hastened, releasing soluble foods so that man's crops flourished and he lived in a comparative abundance previously unknown. Under such conditions he multiplied as never before, calling for more and more food.

Rain pelted down on the bare earth which became increasingly compacted as its organic matter was depleted. The once spongy soil became hard and impervious. Water, with its solutes, was no longer held, but ran over the surface or through the coarse cracks, carrying away the plant foods and suspended soil particles with it. Erosion was violently at work. Rivers once clear became swollen, muddy torrents after rains, only to dry to a thin trickle soon after. What was worse, in many regions where it had lost its water-holding capacity, the soil could no longer maintain the subterranean water supply at its original level, and the water table sank to a lower level. Man learned to irrigate by tapping subterranean water, temporarily alleviating the situation, but at the cost of yet further lowering of the water table. Man learned to produce artificial fertilizers to replenish the minerals leached out of his soils or transported away from them in the form of meat and vegetables, to the massed populations in the cities which housed more and more of his kind. But often he replaced only a part of what he took, and often in an unbalanced form. More machines and more fertilizers masked the depletion of the soil for a while, and land too delicately balanced ever to be broken by the plow was brought under cultivation. Man continued to live in plenty, but he had not yet invented a practical way to restore true balance to the soil. He could add organic matter only in hopelessly inadequate quantities, and his opulent standard of living was bought at the cost of the resources stored in the soil over past thousands of years. Land that is practically irreplaceable is daily being carried to the rivers and thence to the ocean.

It is estimated that today the world has two

acres of arable land for each of its inhabitants. The United States boasts 2.8 acres per capita, and this is considered to be the minimum, or below it, for sustaining our present standard of living. The apparent surpluses now available for shipment to the overpopulated countries of Europe and Asia are extracted at the cost of the future productivity of the land, and over millions of acres our soil is dying. Annually the acreage of available arable land shrinks in the face of a growing population. Europe, excluding Russia, now has eleven million more mouths to feed than it had ten years ago, and this period includes the period of the great war, with all its loss of life. The agricultural methods of civilized man in the United States alone have resulted in the outright loss of over 100 million acres of the best crop and range land, and one third to one half the living topsoil on millions of acres more. And still the rivers are muddy with the soil of our farms. Awakened to the seriousness of this problem, agricultural experts are straining to educate the farmer in practices designed to retard erosion. Plowing is done on the contour, so that the plow furrows are level and act as catch basins for rains. Land is plowed in strips only, with grassy strips alternating, to reduce the amount of run-off. Land too steep for such practices is terraced, and recently huge demonstrations of "soil surgery" were undertaken to awaken the understanding of the people. A dramatically staged restoration of a badly eroded farm of several hundred acres was undertaken with an army of bulldozers, earthmovers, tractors and trucks, and volunteer help. By such means, at enormous cost, a few hundred acres were restored to productivity, all of which might have been unnecessary had man learned sooner the nature of soil, and had he had foresight enough to yield to the pattern set by nature. Even such drastic surgery is little more than a makeshift. The soil washed down the rivers cannot be called back. Strips of sod taken from ridgetops and from some pastureland to hold down the earth of the eroded farm seems much like robbing Peter to pay Paul. Man must see to the conservation of his heritage.

Specific Adaptations of Flowering Plants

In tracing the broad path of the evolution of plants, only brief reference has been made here and there to the special adaptive refinements by which they are fitted into specific and limited environments. Mosses, ferns, and seed plants were considered as though each was a homogeneous group, fitted neatly into a special niche. But this is only part of the story. It is true that mosses are amphibious, ferns less so, and that seed plants as a group are land plants. But a moment's consideration shows that seed plants are found under the most varied conditions, from mountain tops and deserts to the bottoms of ponds. And this brings us to a very significant observation.

Basic and Specific Patterns in Evolution

From time to time, a few basic patterns evolve which must be eminently successful, since they are varied by an almost explosive divergence until they become adapted to a wide variety of limited and special environmental conditions. As a crude analogy to this adaptive radiation, we may consider the evolution of the motorcar. Originally no more than a converted horse-drawn carriage, complete even to the vestigial whip-socket, this sound basic conveyance has evolved into such various forms as the bus, the truck, the tank, the snowmobile, the amphibious "duck," and recently even a car with detachable wings. The unconscious copying of organic evolution is striking when we view a parade of motorcars dating from the beginning of the century. Structures once functional are retained long after their use has vanished, and they disappear or take on new functions only gradually. Thus the dashboard, originally a protection, has become the instrument panel; running boards, once a

necessary step, have receded and nearly disappeared; the trunk, once literally just that, is still noticeable in some cars as a vestigial bustle, though in others it has been streamlined away, but its useful successor, the luggage compartment, still remains. As we shall see in this chapter, surprisingly similar adaptations have taken place in seed plants — adaptations which have sometimes gone so far that the original structure is unrecognizable or even lost.

The Angiosperms: A Basic Pattern

In general, it is not difficult to tell a flowering seed plant from other plants, for all angiosperms have the same basic structural features. Yet only extensive modifications could have produced such extremes as the cactus and the pond lily. Despite these changes, both cactus and pond lily are still flowering plants, for they possess the typical vascular stem and roots, and they produce the highly complex reproductive structure called a flower. We shall see how this basic angiosperm pattern may become adapted to special conditions, changing not only the form or shape of the plant, but sometimes drastically transforming the basic structures of root, shoot, or leaf, at times almost beyond recognition. Not infrequently, these structures come to serve purposes completely different from their original ones. Nevertheless, the basic pattern remains.

THE XEROPHYTES: ADAPTATIONS TO DROUGHT

It is well known that some plants thrive under conditions of dryness where most others would speedily die. Such plants are called *xerophytes* (Gr. *xeros* = dry). Certain forms of cacti live and thrive in regions where rain may fall not more than once in three years.

Clearly, a plant that can live under such conditions must possess special adaptive features. There are many such features, and a typical xerophyte often shows all of them. Moreover, the molding effect of the environment has brought about interesting cases of convergence. Although the cacti, as a group, show more of the xerophytic adaptations than perhaps any other type of plant, numerous others show notable developments of this kind. Cacti and euphorbias, for example, belong to different families, but they have produced similar convergent individuals, so that an untrained observer will frequently refer to euphorbias as cacti. On the other hand, not all members of a group containing xerophytes have become thus adapted. For example, the cactus *Peireskia*, commonly called the Barbados gooseberry (Fig. 194), does not markedly resemble the more typical members of its group. And the euphorbias contain such plants as the poinsettia, the castor plant (*Ricinus*), and the rubber tree (*Hevea*). The Barbados gooseberry may give us a hint of the probable type of less specialized ancestor from which the highly specialized xerophytic cacti have evolved.

Roots of Xerophytic Plants

Root adaptation in xerophytic plants consists mainly of the ability to reach water, to store it in times of abundance, or to retain it once it has been absorbed. Some plants, like alfalfa, send their roots as far as forty or fifty feet below the surface of the soil to regions where at least some moisture is to be found

Fig. 194. The Barbados gooseberry, a slightly modified cactus, gives some idea of the possible appearance of ancestral cacti.

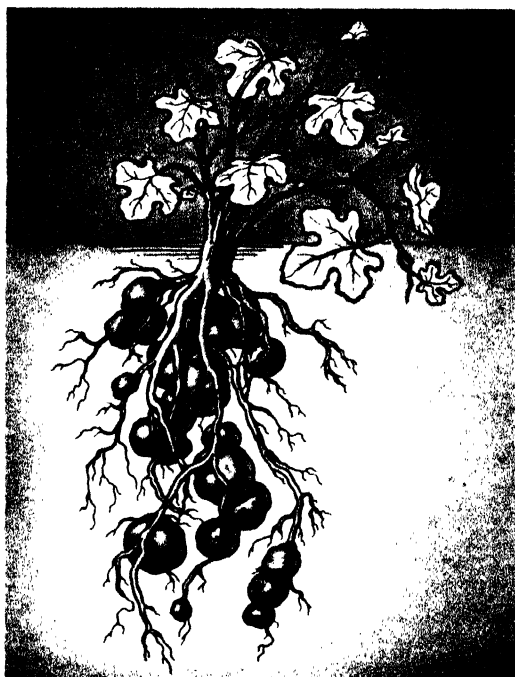
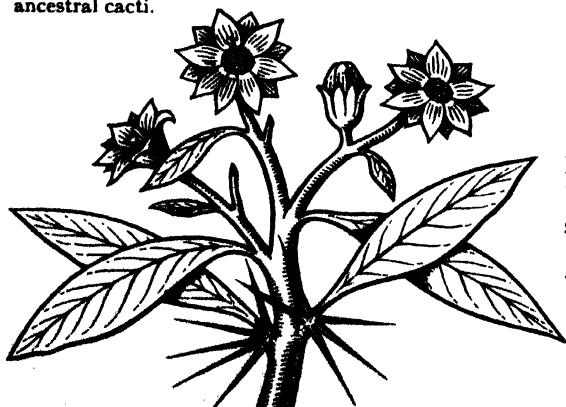


Fig. 195. *Vitis capensis*, a South African grape, showing root tubers.

most of the time. Such a plant has a chance to survive under quite arid conditions without much further modification. The root systems of some xerophytes also excel in their ability to extract moisture from relatively dry soil. Zufi corn, especially adapted to growth on the windy tablelands of New Mexico, sends down unusually long roots immediately upon germination, thus assuring the plant an early start even before the rainy season.

In most cacti, the root systems are so arranged as to take advantage of two sources of water. One part of the system descends almost vertically into deep layers of soil to tap the more enduring sources of moisture. The other is a superficial network of horizontal roots, much branched at the ends and able to absorb large quantities of water rapidly during the brief periods of heavy rains. Other xerophytes, such as the South African grape *Vitis capensis* (Fig. 195) have enlarged root tubers in which both food and water are stored.

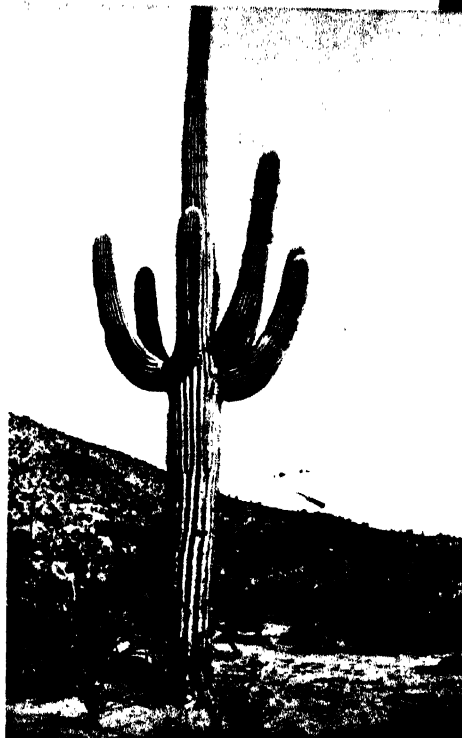
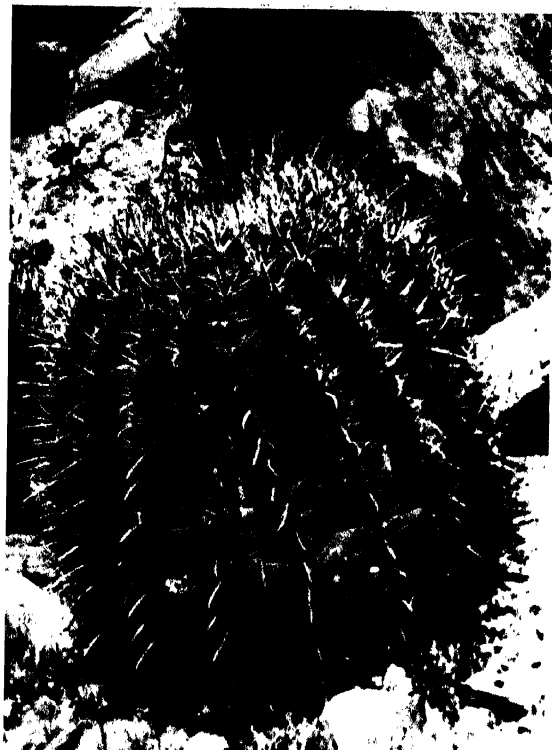


Fig. 196. Barrel cactus, *Echinocactus wislizeni* (left), showing perfected spherical form and accordion pleats. The Saguaro cactus, *Cereus giganteus* (right); the fluted columns of this largest of cacti may rise to a height of thirty to forty feet (Saguaro National Forest, Tucson, Arizona).

Shoots of Xerophytic Plants

Adaptations in the shoots of plants are more obvious than those in the roots, although perhaps no more specialized. Xerophyte shoots may have specially modified shapes. Often they have taken over the function of the leaves, which in many cases have been entirely lost: sometimes they function as storage reservoirs for water. And frequently they show a reduction in surface through which moisture would otherwise be lost. Changes in shape for the last of these reasons eventually approach a sphere, for no other shape offers as little surface for the volume enclosed (Fig. 196). Many fleshy storage stems in the cacti also have accordion-like pleats in their surfaces which are elastic and thus allow variation in the diameter of the stem. When the plant is freshly gorged with water, its diameter increases and these grooves are shallow. Conversely, loss of water causes an orderly shrinking of the plant by a folding of the pleats.

In addition to their change in shape, the stems are green and serve as organs of photosynthesis. Hence they contain guard cells and stomata, but only in limited number. A hard, leathery epidermis further reduces loss of moisture. Since some cacti attain enormous dimensions — the famous Saguaro reaching a height of thirty or forty feet — and may weigh many tons, their woody tissue is well developed. The bristling armament of spines is frequently also a modification of the shoot, though in some plants the spines are modified leaves. It is not likely that spines contribute much directly to water conservation, but indirectly they are of the greatest importance. In arid regions, succulent vegetation is relatively rare and hence desirable to animals and greatly sought after. Spines protect the plant from animals that would otherwise relish it, though — to be sure — such primitive protection is of no great avail against the superior intelligence of man.

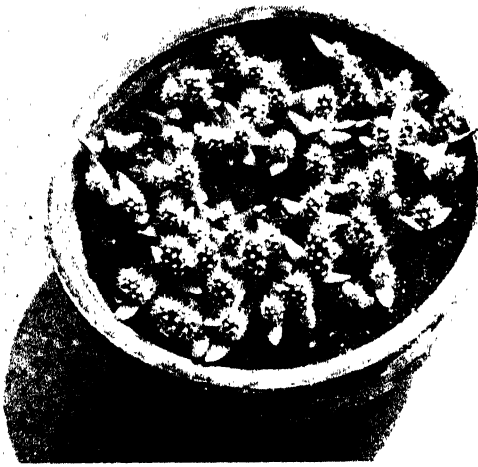


Fig. 197. Cactus seedlings showing leafy cotyledons.

Leaves of Xerophytic Plants

Since dry regions are also usually very sunny, leaf reduction is another common adaptation in xerophytic plants. For leaf reduction decreases surface and, consequently, water loss; moreover, it is possible because such an abundance of sunlight reduces the need for extensive leaf surface. Either the number or the size of the leaves may be decreased, and they may even be completely absent. In the latter case, of course, photosynthesis must be performed by some other part of the plant, usually the stem. The gradual manner in which this change probably took place may be traced in plants whose leaves have been only partly reduced. In the well known crown of thorns, one of the euphorbias, leaves are present but unimportant. In some plants, the leaves are very short-lived and drop off after a brief period of usefulness. The cacti show interesting evidence of their evolutionary descent, for their seedlings produce well-developed leafy cotyledons, although the mature plant entirely lacks leaves (Fig. 197).

Another adaptation to dry climates is the thick, fleshy leaf found in plants like those of the family Crassulaceae, to which belong the common house leek or "hen and chickens"

(Fig. 198) and the mossy stonecrop of Europe. These remarkable plants live under conditions that would appear almost impossible for plant life. Adapted to the dryness of Alpine regions rather than to that of the desert, they cling tenaciously to steep cliffs and rocks, maintaining their succulence even in the scorching mountain sun.

Still another adaptation to drought is found in the fuzzy leaves of the mullein or the rolled leaves of the sandwort, which grow on sand dunes; and finally, in the rolled needle-like leaf of *Empetrum*. Branched tree-like hair cells growing on the mullein leaf cover it with a dense fuzz which helps markedly to cut down transpiration. The leaves of the sandwort roll into cylinders, with the stomate under-surface inside. This surface is even further protected, for its guard cells are set in deep recesses, and each one is further sunk into an individual depression — a triple safeguard (Fig. 199). *Empetrum* similarly rolls its leaves, but the edges, instead of overlapping, are fringed with woolly hairs which interlace and effectively close the seam against any appre-

Fig. 198. The house leek, *Sempervivum tectorum*, has stemless rosettes of fleshy leaves. It grows under seemingly impossible conditions on bare rocks.





Fig. 199. Cross-section of leaf of the sandwort *Arenaria ammophila*, rolled into a tube.

ciable and damaging loss of moisture (Fig. 200).

The ocotillo of our southwestern desert appears to evade drought by the simple method of "closing shop" except during rare periods of sufficient moisture. This bush, of slender gray cane-like stems studded with spines, produces leaves that live only a short while. The rest of the time it simply stands bare, like a tree in winter.

Other Adaptations to Xerophytic Conditions

Other xerophytic plants die back so that only their underground stems or root survive. Still others die entirely as individuals, though the species survives in their extraordinarily resistant seeds. Thus desert regions that do not experience rains more than once in four or five years become clothed in delicate green, later to be sprinkled with a profusion of flowers when the rare life-giving rain awakens the dormant seeds. These plants not only produce enduring seeds, but grow and mature rapidly, and thus are able in a brief period to mature, blossom, and ripen seeds for a new germination which will not grow, perhaps until four or five years later. Random mutations and selection have produced living organisms capable of surviving under seemingly impossible conditions.

HYDROPHYTES: ANGIOSPERM WATER PLANTS

It is in keeping with the random nature of evolution that some land plants should have returned to live in the element from which their primitive ancestors had slowly escaped. It was pointed out in earlier chapters that successful land plants in general have to be more complex than their aquatic ancestors, for the need for differentiation is far less pressing in the water than it is on land. Hence it is not surprising that plants which have reverted to the water show special adaptations that are in many cases not new mechanisms, but simply represent the loss of structures which their ancestors had evolved.

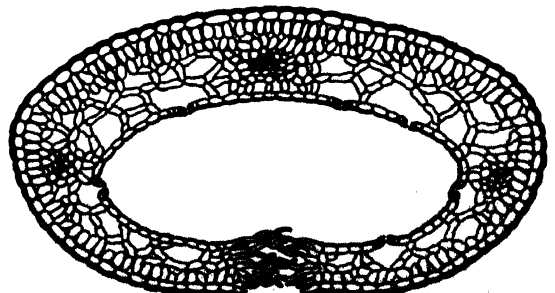
Roots

Since there is no great need for firm anchorage and little need for absorption from the soil, water plants generally show regression in their root systems. In some cases the root may be entirely absent. Indeed, the easy living conditions in the water have produced results comparable to those of parasitism: a gradual loss of structures and organs, and finally a reversion to the simple thallus structure seen in early aquatic plants. These plants follow the course of "drifters" rather than that of "fighters."

Shoots

Like the roots, the main and secondary shoots or stems of hydrophytic plants are generally reduced in complexity. The fibrovascular cylinder is usually poorly developed, particularly the xylem. Since the plant is largely supported by water, the violent mechanical stresses such as those caused by storms do not

Fig. 200. Cross-section of *Empetrum* leaf, rolled in the form of a tube, with the stoma inside. Where the edges of the leaf meet, a mass of woolly hairs interlaces.



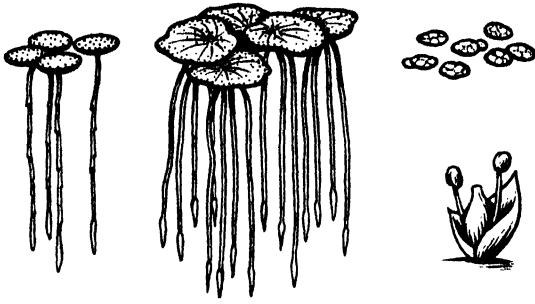


Fig. 201. Various Lemnaceae, greatly simplified as a result of a hydrophytic life: Left to right: Common duckweed; large duckweed; *Wolffia*, which has no roots. At lower right is the flower of common duckweed. Simplified roots of duckweed retain root caps.

affect it, and hence fibrous or woody structures lose their selective value and tend to disappear. Instead, a cheap device — cheap in the sense that it does not place great demands on structural tissue — which lifts the leaves towards the surface and toward light, is adequate. So the stems of many aquatic plants have large air chambers, or are porous and spongy. Moreover, there is no protective epidermal tissue, and the stems are frequently long and slender.

Leaves

The leaves of hydrophytes are usually very thin and much dissected. Perhaps their form endows the plant with special advantages, or possibly they represent a sort of reversion due to simplification of demands. There is also the ever-present possibility of non-adaptive changes genetically linked to advantageous ones. Perhaps all these things play a part. Thus the thinness of the leaves may be due to the fact that there is no need for heavywater-preserving tissues. It may also represent an adaptation to the reduced penetrating ability of sunlight under water. And their dissection may be an adaptation for absorption from the water, enabling them to take over some of the work of the reduced root system.

The extreme regression shown in the Lemnaceae is worth special consideration. These are the common duckweeds that sometimes cover ditches and ponds with masses of green, disk-

like leaves. Most of them consist of no more than a leaf with a simple hanging root attached to it, and some have been reduced to a structure that is hard even to recognize as a leaf and have entirely lost the root. Yet these tiny plants, some no more than $\frac{1}{16}$ inch long, still produce blossoms — though these too have been simplified to an almost irreducible minimum (Fig. 201). In one of them, *Wolffia*, the entire plant consists simply of a microscopic sphere of cells, possibly a reduced leaf, and yet the plant is able to survive under modern conditions. Perhaps, except for the changes in its animate environment, other outside conditions are little different from what they were at the beginning. Most of the duckweeds survive in the face of more complex rivals by the sheer pressure of numbers achieved by means of their enormous reproductive capacity through simple, asexual vegetative methods.

EPIPHYTES: PLANTS THAT GROW IN THE AIR

Various kinds of plants, many of them angiosperms, grow upon other plants, living or dead, but without drawing upon these for any other service than support, and without contact with the soil. Such plants are called *epiphytes*. The term is somewhat loosely used, and it may or may not include vines and algae lodged in trees. Generally it relates to plants that have no attachment with the ground, yet neither draw food from the plant upon which they have lodged, nor benefit it in any way. Some queer combinations of mutations and environmental conditions must have made these plants air dwellers. Such plants include many of the orchids, the Spanish or Florida moss (*Dendropogon usneoides*), and the related air pines (*Tillandsia*). That they obtain no supplies from the supporting plant is evident from the fact that they are nowadays frequently found growing on telephone wires. Roots, shoots, and leaves of such plants are frequently modified in an astonishing manner. Many epiphytes, such as the orchids, have aerial roots covered with special layers of air-containing cells — the *velamen* — that are exceptionally absorbent and able to retain moisture once it



Fig. 202. Aerial roots of an orchid (*Dendrobium nobile*), showing the white velamen covering which aids in rapid absorption and retention of water.

has been absorbed. The air enclosed in the outer tissues of the root gives these plants a characteristic white or silvery appearance (Fig. 202). The *Florida moss*, a highly specialized rootless plant, grows in festoons on trees. Its slender stems and leaves are covered with gray, scale-like structures which absorb water from the moist air. Neither this plant nor the "mosses" which festoon the trees of northern woods are real mosses. Florida moss is a monocotyledonous plant related to the pineapple, and the "moss" of the northern forests is a lichen — a combination of alga and fungus.

Other members of the pineapple family, the air pines, such as *Tillandsia*, look very much like the tops of pineapples. The air pine catches rain-water in its crown, and special hair-like processes within this receptacle absorb the water for use by the plant (Fig. 203). From modes of life such as this, it is not a great step to mutualism, symbiosis, or parasitism.

ADAPTATIONS TO THE LIVING ENVIRONMENT

Every living organism influences and is in turn influenced by other living organisms. Often such mutual relationships are of major importance, and so have caused profound changes in shape, structure, and chemical composition. We may consider the chief of these

adaptive relationships under the following headings: (1) *mutualistic* or *symbiotic*, in which organisms live together in more or less intimate association, usually to their mutual benefit; (2) *parasitic*, in which there is an intimate association to the benefit of one and the disadvantage of the other; (3) *saprophytic*, in which plants derive their sustenance from dead and decaying organisms or the wastes of living organisms; and (4) *carnivorous* or *insectivorous*, in which plants supplement their food supply by digesting and absorbing small animals.

The relationship between organisms may range from casual contact to complete interdependence. Somewhere between these extremes, an arbitrary line may be drawn beyond which the relationship is close enough to be called mutualism or symbiosis. As this line is largely a matter of choice, much confusion unfortunately exists in the use of these terms. Mutualism is the term generally applied where the relationship is external; symbiosis where it is internal or intermingled. To illustrate, the relationship between algae and fungi in the lichen is definitely symbiotic. That between insects and flowers may be termed mutualistic, although more typical cases of mutualism are found among animals. Probably the various forms of symbiosis and parasitism arose from an earlier mutual relationship or from a saprophytic habit. Indeed, these things can be explained in no other way.

Insect-Flower Relationships

Despite the highly specialized and precise relationship between insects and flowers, it is often considered too impermanent to be classed as symbiosis, and instead is generally referred to as mutualism. For intricacy and perfection, however, some of these arrangements can hardly be matched anywhere else in the world of life.

Cross-pollination is of the highest evolutionary importance, because it brings about the mixing of the genes from two different streams of germ plasm, and this importance is emphasized by the perfection of the methods which plants have evolved to achieve it. So astounding

ing are some of the devices which have been evolved to assure cross-pollination that it is difficult to imagine how random mutation and selection could have produced them, and yet indications are numerous that they have indeed been produced in this manner. Not all such devices are complex, however, and in fact some of the simplest are often the most successful, whereas some of the most inordinately complex ones appear to be least successful, as the scarcity of certain orchids emphasizes.

To begin with, the fact that the color and scent of flowers attract insects is in itself a remarkable evolutionary adaptation. The sugary solutions called nectar, which are secreted by flowers and attract insects, represent a definite expenditure of energy by the plant, and must be considered a tribute paid by the flower to the insect in return for its service as a pollen bearer. In order to have selective value, the

Fig. 203. Air pine, *Tillandsia*, growing on a tree in Florida. There is no organic connection between the air pine and the supporting tree.

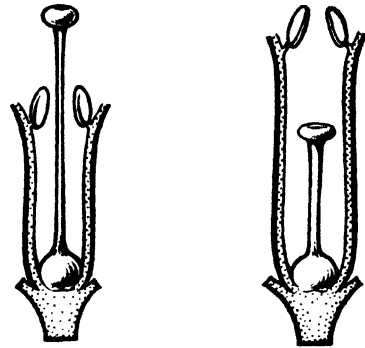


Fig. 204. Dimorphic flowers of Chinese primrose (*Primula sinensis*). Left: Flower with long style and with stamens low in the corolla. Right: Flower with short style and anthers high in the corolla.

return must, of course, be greater than the outlay. The instinctive reaction of the bee serves the needs of the flower, and one must know something about each to understand the other.

Bees generally, although not without exception, seem to have one-track minds when it comes to visiting flowers. A bee that has started on one kind of flower generally continues to visit the same kind and to ignore the others. This is to the advantage of the flower, since it avoids the waste of pollen which would occur if bees carried it to other species of flowers. The bees, too, may indirectly benefit, since better pollination produces more seeds and hence more of that kind of flower in the following season. But this preference of a bee to visit just one kind of flower is not in itself sufficient to insure cross-pollination, which occurs only when pollen produced by one blossom is transferred to the stigma of a blossom on another plant of the same kind. For bees may transfer pollen between blossoms on the same plant.

Cross-pollination is greatly furthered by dimorphism or polymorphism in blossoms. The flowers of the Chinese primrose, for instance, are dimorphic. That is, they are two kinds, each on different plants: one kind has a long style and short anthers, while the other has a short style and long anthers (Fig. 204). As the bee crawls into a blossom to obtain the



Fig. 205. Floral mechanism in geranium tending to reduce probability of self-pollination. When the flower first opens (1, 2, 3), the anthers open and shed their pollen, while the stigma remains closed. When pollen is gone, the stigma unfolds and becomes receptive (4, 5).

nectar at its base, it will pick up pollen on its head or thorax from the blossom with short anthers. The pollen on this part of the bee's body will be in the proper position for transfer to the short-styled blossom. Conversely, the pollen dusted on the abdomen of the bee from the long anthers of that sort of blossom is most likely to be brushed against the long style of the opposite sort of blossom. This kind of selective pollination is sometimes further restricted by the peculiar fact that pollen from short anthers does not germinate as readily on short styles as it does on the long ones, and vice versa. In some blossoms, instead of two different lengths of styles and anthers, there may even be three, as in the pickerelweed (*Pontederia cordata*).

Another relatively simple way in which cross-pollination is furthered is found in the geranium. Here the anthers ripen first and shed their pollen while the stigma is still immature and closed. After the pollen has been shed and carried to other, older blossoms with receptive pistils, the stigma ripens and may receive pollen carried to it from other, younger blossoms (Fig. 205). This does not prevent self-pollination between different flowers on

the same plant — but it operates statistically. In other flowers, as in the figwort, the process may be exactly the reverse, the stigma of one flower maturing and receiving pollen from other blossoms before its own anthers release their pollen. Also unspectacular but efficient is the chemical antagonism between the pollen and the secretions of the stigma within a single blossom. In many species, pollen will either not be stimulated to germinate on the stigma of its own blossom or of any others with the same "sterility gene," or also the secretions of the stigma may actually have a toxic effect on the pollen, as in certain orchids.

Even greater refinements are found in the methods of transferring pollen to the carrier and again from the carrier to the stigma. In *Salvia*, for instance (Fig. 206), the stamens are hinged, curved organs somewhat like powder-puffs on long handles. When the bee enters the flower, it is forced to press against a projection at the base of a stamen, whereupon the stamen swivels on its hinge so that the anther at its tip is lowered and pats the abdomen of the bee, thus dusting it with pollen. At this time the stigma is still unripe and hidden in the upper folds of the blossom. If the bee now



Fig. 206. *Salvia*, an effective mechanism for pollen transfer. 1. Early stage. Anther (*a*) and style (*s*) are hidden within the upper lip. 2. Young blossom. A pencil inserted along the path of the entering bumblebee depresses the base of the anther. Normally this dusts the abdomen of the insect with pollen. 3. Older blossom in which pollen has been shed. The stigma now occupies the former position of the anthers, thus picking up pollen from an insect that has visited a younger blossom.

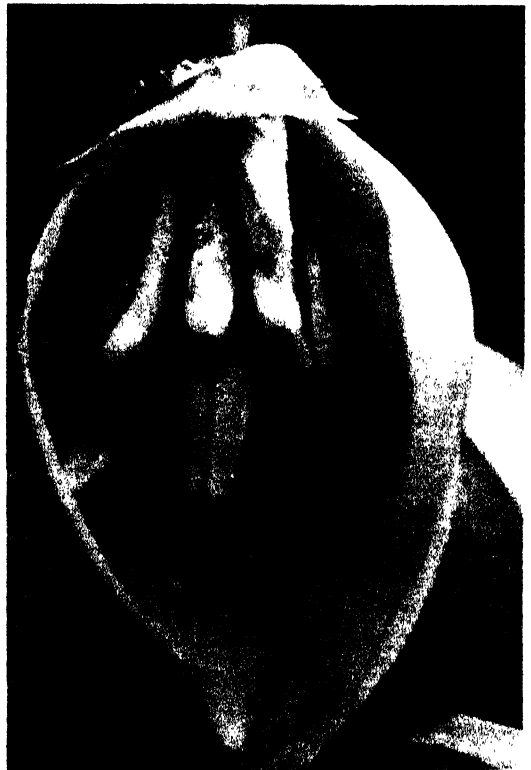
moves on to an older blossom, it finds the anthers empty, but the stigma, opened out into a two-pronged organ, hangs down in the path of the bee in such a position as to brush it exactly where it had previously been dusted with pollen by the anthers. This hinged stamen that does its work so perfectly is truly remarkable, and yet it is by no means unique.

Sir Francis Darwin, son of Charles Darwin, and a distinguished botanist in his own right, compared the coordination between flowers and the specific insects that fertilize them to the relation between a lock and a key. In many cases this is very apt. Thus the fig wasp (*Blasitophaga grossorum*), actually a parasite in the fruit of the Smyrna fig, is necessary for successful pollination of the blossom. Early attempts to grow Smyrna figs in the United States, as well as in Australia and South Africa, were total failures because the role of this minute insect was not understood. The process is complicated, but essentially the services of the insect

consist in emerging from the fruit of a male, or caprifig, where it has spent its larval life, at the proper time to pick up pollen and transfer it to the stigma of a flower of the female fig.

The yucca, a member of the lily family, shares with an insect — the yucca moth (*Pronuba yuccasella*) — such a fantastic partnership as to baffle our best explanations (Fig. 207). For each is completely dependent on the other and perfectly adapted to it. The large waxy-white yucca flowers produce a sticky pollen that cannot be picked up by the wind, and since it is produced on long anthers that hang well below the style of the drooping blossom, the pollen cannot drop onto the stigma. Self-pollination

Fig. 207. *Yucca* flower, in section, and moths. Acting with instinct that seems almost to be reasoning, the yucca moth after laying her eggs in the pistil of the flower molds a mass of pollen and places it on the pistil to insure fertilization. The larvae eat only part of the seeds. Both plant and insect benefit by the relationship.



is further made impossible because of the construction of the pistil. This is tubular, and the stigmatic portion of it is confined to the inner lining of the tube. To germinate, the pollen has to be transferred to the very inside of the style, and thus even artificial pollination is difficult. At the exact season when the plant flowers, the pupa of the yucca moth, which has wintered in the ground, releases its imago, or adult moth. The female moth, once she has mated, flies to a blossom at dusk, gathers pollen from the anthers, rolls it into a sticky ball, and then flies to another blossom. Here she inserts her ovipositor into the ovary of the flower and lays a number of eggs among the ovules of the plant. Then she crawls to the end of the pistil and stuffs the pollen ball into the tube-like style, thus insuring the pollination of the blossom and the ripening of the seeds. The eggs she has laid eventually hatch, and the young larvae begin to feed on the young seeds, but the moth never lays so many eggs in one flower that all the seeds are eaten. The larvae, having reached full growth, descend to the ground by means of threads which they spin, burrow into the ground, and eventually pupate. The ripened seeds that are left are also scattered, and the cycle is ready to begin once more. Neither organism can live without the other.

Other Symbiotic Relationships

Spines of certain African acacias have swollen hollow bases which are regularly inhabited by ants which fiercely resent any attempt to handle the bush rudely. Although both bush and ant can live independently of each other, there appears to be here at least an incipient relationship. A similar one is found in other plants, such as that between *Endospermum formicarum* and the ant *Camponotus quadricaps*, which establishes colonies in the hollow stem of the plant.

Much more intimate, and of unquestioned mutual benefit, is the relationship between various forms of fungi and seed plants. Many forest trees depend on certain mycorrhizal (Gr. *mykes* = fungus + *rhiza* = root) fungi for effi-

cient root absorption. A similar relationship between orchids and certain fungi which infect their roots has been clearly established by the classic experiments of Noel Bernard. Attempts to grow orchid seedlings in sterile cultures or on ground uninfected by the proper fungus usually fail. But if the appropriate fungus is added to the germinating seed, growth proceeds normally. It may be for this reason that orchids usually grow in colonies and do not easily establish themselves in new localities, even when all conditions appear to be favorable.

The mycorrhizal relationship between plants and fungi is not limited to angiosperms, for certain gymnosperms, such as pines, are similarly dependent. In such associations, the fungus obtains organic compounds from the plant, while the plant is aided in its absorption of minerals, especially compounds of nitrogen, since the fungus has the ability to fix atmospheric nitrogen. This nitrogen-fixing ability depends on the association of the fungus with the roots of the seed plant. Although there is reason to believe that neither organism is absolutely dependent on the other, it appears that life is made easier for both by their association. Specifically, the soil conditions under which they can grow are much more limited if the fungus is excluded.

A similar nitrogen-fixing service, it will be remembered, is performed by the bacteria which live in the nodules of the roots of legumes, such as peas, clover, and others. The fern *Azolla* has established a symbiotic relationship with the blue-green alga *Anabaena*, which also has the ability to fix atmospheric nitrogen.

Parasitic Angiosperms

Parasitism, in which the plant obtains part or all of its nourishment from another living organism upon which it lives, is rare among angiosperms, but does exist. It is surprising that parasitism is not more common, for the intimate relationships between plants growing in their natural environment appear to be ideal for the favorable selection of mutations which would develop parasites. Vines, such as the

morning glory and the grape, and epiphytes such as the Spanish moss, appear to be in a particularly favorable situation for the development of parasitism. To a limited degree, such plants have already entered upon the road to parasitism, for they depend on other plants at least for support, if not for nourishment. When we consider the experimental evidence which shows that many plants can grow in a total absence of light if supplied with solutions of sugars and other nutrients, it becomes clear that the conditions for the development of parasitism are all prepared. It requires little imagination to see how the symbiotic relationships described may likewise become unbalanced and lead to parasitism.

The common mistletoe (*Phoradendron*) is unquestionably a parasite, although it appears to limit its demands upon its host to a supply of water and nutritive salts, while it carries on at least a part of its own photosynthesis, as testified by its pale green leaves. Mistletoe grows in the form of shrubby clumps on the branches of a rather wide variety of trees. It has specialized rootlets, or *haustoria* (Lat. *haurire* = to draw, drink), which penetrate the branches of the host and make contact with the vascular bundles (Fig. 208). Under unusual conditions, mistletoe has been found capable of manufacturing sugar for the host upon which it grows. Thus it has been observed that in a group of defoliated trees, those which had mistletoe growing on them were able to survive while the others died. It is difficult to say why mistletoe has not yet evolved into a complete parasite, for except in such unusual cases as that just described, it is not clear what the mistletoe has to gain by continuing to manufacture its own sugar. In other words, the possession of leaves and the ability to carry on photosynthesis does not appear to have great selective value for the plant. This being the case, we have reason to believe that some day mistletoe may be a full-fledged, leafless parasite, provided that this does not lead to the extinction of its host species.

Such a full-fledged parasite is the dodder (*Cuscuta*), also quite aptly called devil's twine,

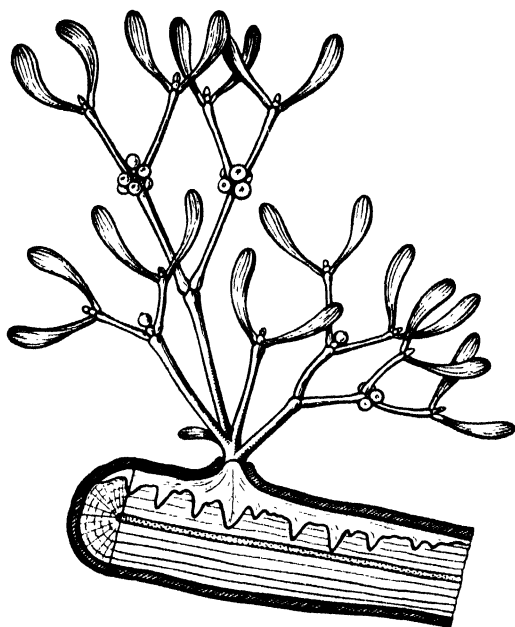


Fig. 208. The mistletoe, a parasite, showing haustoria penetrating tissues of host.

a member of the morning glory family. Like the mistletoe, the dodder produces haustoria that penetrate the tissue of its host and make contact with both xylem and phloem. In view of what we now know about evolutionary processes, we can expect organs and structures which no longer are "necessary" and so have no further selective value, to disappear. The dodder meets this expectation in full measure. The plant is a yellowish-orange color, since it produces no chlorophyll. Its leaves have been reduced to functionless scales; roots are absent, except for the modified aerial roots, the haustoria. Capable of rapid growth in length, the plant soon completely covers its host with a tangled network of glistening, thread-like stems. The dodder seedling, upon germination, is a slender worm-like structure, entirely dependent on its reserve food supply, since it can produce no chlorophyll. It even lacks cotyledons. The length to which the seedling may grow is thus strictly limited by the amount of its stored food. In many cases, this length is not sufficient to bring the tip of the seedling into con-

tact with a possible host. But as the tip grows, the posterior portion of the plant shrivels and dies and the nutrient substances obtained from it are transferred to the growing tip, enabling the plant to crawl along the ground by dying at one end and growing at the other. During all this time, the tip performs snake-like gyrations, ideally suited to bring it into contact with the stem of a growing plant. If it does not soon succeed in this, however, the seedling dies entirely.

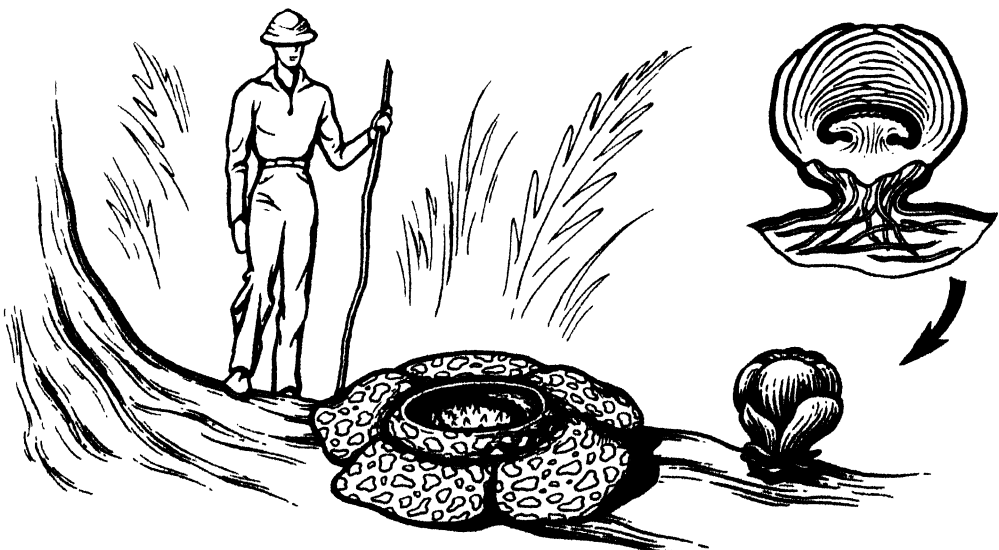
Competition among Plants

Only our slow perception prevents us from realizing the intensity of the competition between plants. The struggle between seedlings of the dodder and those of its near relative, the morning glory, recorded by a time-lapse camera, is a sight never to be forgotten. Both plants perform gyrations as they grow, and both do so in order to gain support from some other plant. For a brief period, the gyrations of the morning-glory prove to be successful as evasive tactics, and we can see it repeatedly escape the strangling hold of the dodder. But eventually poor timing on the part of the morning

glory gives the dodder its first hold, and from then on the battle is lost and the morning glory eventually dies.

The cancer-root (*Thalesia uniflora*), common in meadows and woods from coast to coast, is a leafless plant which obtains its sustenance by means of a parasitic root system which attaches itself to the roots of neighboring plants. A similar root-parasite is the Malayan species *Rafflesia*, of such parasitic perfection as almost to excite admiration. The body of the plant has been reduced to a mycelium-like mass which penetrates the tissues of its host, a vine (*Vitis*). No portion of the parasite is visible from the outside, and yet it eventually gives ample evidence of its nature as a seed plant. In time there appears on the exposed root of the host plant a swelling which may reach the size of a cabbage before it unfolds. When it does, it proves to be a flower up to three feet in diameter. Its odor is that of carrion, and carrion flies act as pollinators. This plant illustrates perhaps the extreme of angiosperm parasitism, for all structures but those essential to reproduction and parasitic nutrition have been eliminated (Fig. 209).

Fig. 209. Blossom and bud of the parasite *Rafflesia*, growing from root of a host plant. Section of bud shows haustoria penetrating host. The man at the left shows the immense size of the blossom.



Saprophytic Angiosperms

Saprophytes, common among the fungi, are relatively rare among angiosperms. They differ from parasites only in that they obtain organic compounds from dead tissue instead of from living. The borderline between these two forms of nutrition is a delicate one, and many a saprophyte may at times become a parasite simply by "jumping the gun" and starting its digestive processes before the material it is digesting has quite ceased to live. Perhaps the best known of our angiosperm saprophytes is the Indian pipe, *Monotropa uniflora* (Fig. 210), which is sometimes clearly parasitic. Lacking chlorophyll, it is pearly white, and despite symptoms of degeneration, it never fails to excite admiration because of its unusual aspect and grace. A closely related plant, the pinesap (*Hypopitys*) has a buff or pinkish color and bears red or yellow flowers. Like the Indian pipe, it has no chlorophyll and is saprophytic.

Carnivorous Angiosperms

Perhaps the strangest of all modifications of structure are found in the most unusual of all angiosperms, the carnivorous plants. Many plants have been shown to be capable of utilizing organic foods, if these are presented in the proper manner; hence it is not surprising that some plants have evolved structures whereby they can obtain and prepare organic foods for their use. Saprophytes do this unspectacularly, parasites more strikingly. But the methods of the carnivorous plants have to be seen to be believed. Such plants are Venus's flytrap (*Dionaea*), the sundew (*Drosera*), the bladderwort (*Utricularia*), the pitcher plants (*Sarracenia* and *Nepenthes*), and many others. These plants all possess one characteristic in common: they catch insects, digest them, and absorb the juices. They do this by means of leaf-modifications, but in a great variety of ways (Fig. 211).

In Venus's flytrap the terminal portion of the leaf is divided and hinged, much like the two covers of a book; this is the trap. The edges of the hinged covers are fringed with



Fig. 210. The saprophytic Indian pipe (*Monotropa uniflora*), with leaves reduced to functionless scales, is common in eastern woodlands.

bristle-like hairs. On the open surface of the trap are three pairs of short spines which act as trigger hairs. When an insect steps on or brushes against these spines, in a matter of seconds the covers fold together, trapping the insect between them. For a plant, the action is amazingly rapid, though rather slow compared to animal motion. But the action is so smooth and gradual that insects are frequently captured. When one is caught, the margin of the leaf exudes sticky digestive fluids which digest its body. The sundew reacts in much the same way, except that the insect is captured by tentacle-like processes on the leaf, each with a sticky, glistening drop at its tip, which fold over the prey.

Less spectacular only because it is smaller is the bladderwort. This plant grows in abundance in many stagnant pools, and attached to the tips of some of its submerged branches are wonderfully modified leaves which are perfect

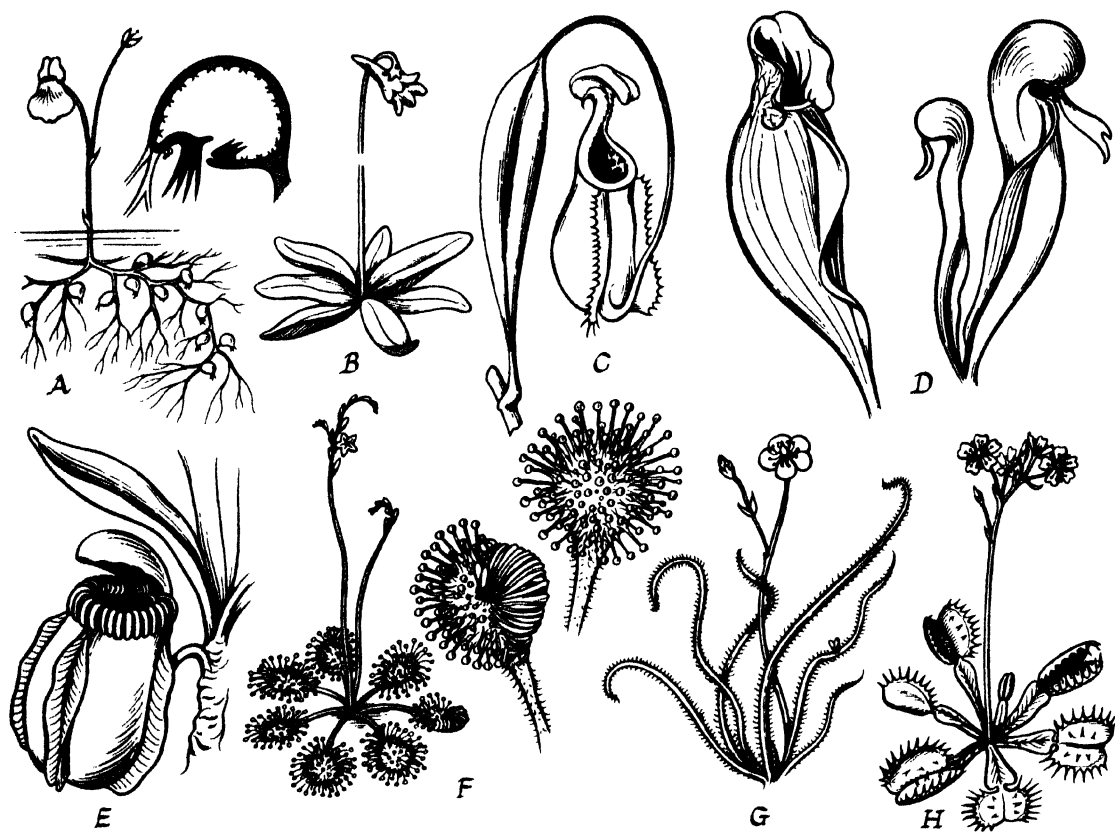


Fig. 211. Insectivorous plants, in which modified leaves are insect traps. *A.* Bladderwort. *B.* Butterwort. *C.* Leaf of tropical pitcher plant. *D.* American pitcher plants. *E.* Australian pitcher plant. *F.* Sundew. *G.* Flycatcher. *H.* Venus's flytrap.

insect traps. The trap is a small globular bladder with an opening at its lower end, guarded by a trapdoor of bristles which may be pushed inward. Any small organism may thus swim in, but the bristles cannot be pushed outward, and so the creature cannot swim out again. Since specialized digestive cells line the cavity, the rest of the story need not be told.

Probably no plant structure is more fantastic than the mostly tropical pitcher plants, the *Nepenthaceae*. The American pitcher plant (*Sarracenia*) has a curious structure, but its refinements are not equal to those of the tropical forms. From the climbing stems of *Nepenthes*, leaves develop that show a remarkable degree of differentiation and specialization. The main blade of the leaf is broad and green and performs its normal functions. But the tip continues as a long tendril-like appendage, at the end of which it flares out to form a highly

perfected insect trap. It is doubtful whether the human mind could much improve on its refinements. This trap consists of a jug-shaped vessel, open at the top, but protected by an overhanging roof — also a part of the leaf — against flooding by rains. The rim of the open jug flares out and is brilliantly colored to resemble a flower, and to add to the temptation, honey is exuded around its rim in sufficient quantity to glitter in the sunlight. The inside surface of the pitcher is slippery and is lined with downward projecting hairs, and its bottom holds a watery solution. Insects, attracted by scent and perhaps color, explore the interior of this “flower,” but soon are trapped at the bottom of the pitcher, from which there is no escape. Its narrowness precludes escape even by flight. Digestive juices in the water do their work, and the insect becomes incorporated into the structure of its host. Only flowers can

match in perfection these truly wonderful leaf modifications.

ANGIOSPERM MODIFICATIONS AND MAN

Man himself has been one of the environmental agencies which, through a selection of natural and even of induced mutations, have produced the endless varieties of plants that exist today. That plants have been fitted into almost every conceivable kind of environment eloquently attests to the rich possibilities inherent in them. In most cases, where man has not been the agent, a plant has survived exclusively because of its ability to hold its own against all living competitors as well as against the onslaught of inanimate forces and conditions. In a few cases plants have survived for qualities that tend to favor other organisms than themselves — in true symbiotic relationships — though even here the fact that an organism benefits another eventually also benefits the organism itself. Thus man is not the only creature to shape another to his own advantage; but his achievements in this field are vastly richer than those of any other organism.

In a broad sense, all of life is one vast symbiotic or mutualistic complex, for each organism is influenced by others and in turn influences others. But the relationship between agricultural man and his domesticated creatures, including plants, is much closer to mutualism, or even symbiosis, than is that of organisms in general. Through the use of his selective powers, man has been instrumental in evolving plants that answer his desires and fulfill his needs. We have evidence that this process has been going on for tens of thousands of years, at first probably unconsciously, but more recently in full awareness of what was being accomplished. As a result, the domestic plants of today have evolved into forms fitted almost as precisely to man as the yucca plant is fitted to the yucca moth. Man is more flexible and versatile than his plant partner, and since he does not depend on any one plant variety only, he is less dependent on it than the plant is on him. In many cases the plants are

entirely dependent on man their creator and have entirely lost their ability to shift for themselves. Thus maize, with its seeds enclosed in the husks that surround each ear, could not disperse its seeds if left to itself and would soon be extinct. Even as the yucca moth benefits the plant despite the fact that the larvae eat many of its seeds, so man benefits even the food plants which he has evolved so that he may eat them. For as the moth by instinct lays so few eggs in each ovary that the larvae do not eat all the seeds, so the gardener consciously spares enough plants or seeds so that the species will continue. Without man, domesticated plants would become extinct in a few years. A modern garden of vegetables and flowers, left untended for a few years, would revert to weeds, leaving scarcely a trace of the domesticated plants it once contained.

Root Qualities Desired in Domesticated Plants

Roots have long been used by man. In many plants, the roots serve as a reservoir for the storage of organic compounds over the winter, and thus make it possible for the plant to obtain an early start in the following season. It is this very concentration of organic foods that makes a root of value to man. In order to make use of these substances, man usually eats the entire root. In such cases, the qualities sought are a maximum amount of stored food and a minimum of fibrous and vascular tissue, which makes the root stringy and tough. Roots so used also lack miscellaneous compounds that are poisonous or distasteful, and the roots preferred contain compounds that make them palatable. Many of the useful roots fill these requirements. Thus in turnips, beets, parsnips, radishes, carrots, salsify, and sweet potatoes, the fibrous components of the fibrovascular bundles are at a minimum, and the texture is tender and brittle. In some roots, such as carrots and parsnips, strong flavor has been reduced by careful selection. Many compromises have been made, since it has frequently been found impossible, for the present, to incorporate

all desirable traits in a single plant. Thus carrots which are tender and sweet, because of their delicate texture do not keep well in storage and do not give the maximum yield per acre. On the other hand, where flavor is less important than storage quality, carrots have been produced that give a tremendous yield per acre and store well. These are best for feeding to livestock.

Celery has been transformed from its coarse, rank-tasting wild form to the delicious, tender-stalked plant we know today. In this case we care little about the root, except as it performs its natural function. However, in the variety known as celeriac or turnip-rooted celery, the quality of the stalk has been ignored, while the main stress has been placed upon producing a thick, fleshy root which can be used as a vegetable in stews and salads. Celeriac is thus an excellent example of plants in which structures, originally less important, have been transformed into structures of main importance, so as to produce plants widely differing from each other in appearance and use, despite their close relationship.

In warm climates, the roots of major importance are the sweet potato, the yam, and the cassava, for these provide the bulk of the carbohydrates in the diet of large parts of the world's population. In these plants selection has been for less fiber, greater yield, and better flavor, by human standards.

Other roots, which yield specific chemical substances, have been selected for their ability to provide greater concentrations of those compounds. Among the list are *aconite*, a cardiac and respiratory sedative; *gentian*, used in dyspepsia and intestinal catarrh; *licorice*, a soothing agent and a laxative; the purgative and astringent *rhubarb*; *sarsaparilla*, common in soft drinks, but also used as a diuretic and for other medicinal purposes. These are but a few of a very long list. Of recent importance in our war against insects are *pyrethrum*, obtained from the roots of the chrysanthemum *Pyrethrum roseum*, and the now common *rotenone*, obtained from the cube and derris roots of South America.

Shoot Qualities Sought in Domesticated Plants

Shoots are widely varied and man has utilized them for a great many purposes. In potatoes we desire prolific tuber production, far beyond the natural needs of the plant, and we have very specific ideas of what sort of tubers we wish. We want the fibrous tissue reduced as much as possible, the starch smooth and well flavored, and the lateral buds on this highly modified stem to be inconspicuous and not too numerous. Again, since one plant cannot answer all our demands, different varieties of potatoes have been evolved, some adapted to different kinds of soil, some early, some late in reaching maturity. In trees, less "improvement" has been achieved than in most other plants, primarily because of their slower growth. But even the problem of slowness has been attacked, and species of poplar have been produced that yield more wood in less time by growing more rapidly. Mutations have been favored which produce a swollen stem in certain species of cabbage, so that instead of raising the plants for leaves, as is done with the more normal varieties, we raise them for their stems. These are the kohlrabi, better known and valued in Europe than here. Broccoli is a cabbage selected for its edible flower buds.

Cannabis sativa, the hemp plant, is grown not only for its bast fibers, which are used for twine and rope, but also for its resins, which contain compounds used in drugs. This is the plant from which hashish is obtained, used as a narcotic and an intoxicant. Because of its variable quality, the raw drug is not favored for medicinal purposes, though selective breeding could undoubtedly produce a plant capable of yielding a more uniform and superior drug. Fiber production, on the other hand, would require selection for an entirely different set of mutations.

Linum usitatissimum, the flax plant, has also been selected for the fiber obtained from its stalk. The annual flax now grown has been under cultivation for not less than five thousand years, and its origin is obscure. *Linum angustifolium*, a smaller plant, was probably

the earliest cultivated flax, and has been used by man for at least ten thousand years, extending back into neolithic times. It is therefore not surprising that a plant so long cultivated should have been brought to the point of producing fibers of such excellence.

Leaf Qualities Desired

The same principles that activated man in selecting plants for specific root or shoot structures also guided him in his selection of leaf structures. Leaves that serve as food were of course selected for lack of fibrous structure and for flavor. Lettuce, for instance, perfectly answers these demands. Where most beets are selected for their root structure, Swiss chard, a form of beet, has been selected for its large tender leaves. Cabbages represent selection for bulk of leaf formation and shortness of stem. Celeriac, previously mentioned, was selected for its root structure while celery has been selected for its delectable petioles. Still other leaves are selected for the drugs and oils they contain. A few of these are spearmint, peppermint, tea, and tobacco. There are, of course, many others.

Flower, Fruit, and Seed Qualities Sought

What people want in flowers is so well known that we need not discuss it in any great detail, though the rewards reaped by those who have sought to realize the desire for larger, more ornate, and more varied flowers may be pleasantly reviewed in any large seed catalog. If scent was good, it was accentuated; if bad, it was eliminated. Not satisfied with a single corolla of petals, horticulturalists have bred many "double" blossoms. An interesting result of such efforts is the fact that plants once markedly dissimilar are growing more and more to resemble each other superficially. This is clearly a case of convergence, and the environmental factor responsible for it is man. Thus many marigolds now strongly resemble chrysanthemums; zinnias look like marigolds; and there are dahlia-flowered zinnias — and balsam that looks like roses — to mention only a few.

Perhaps of greater importance are the changes brought about in fruit and seed. Here too reference can be made only to the general trend. Aroma, size, color, texture, time of ripening, and many other qualities have been sought in plant breeding, and often successfully. Since in many cases it is impossible to combine all desirable traits in one fruit, innumerable varieties have been produced. Thus there are summer apples which ripen early, but unfortunately they are perishable and poor in quality. There are fall apples unsurpassed in quality, but these also do not keep too well. And finally there are winter apples with thick, waxy skins that protect the fruit far into the following spring, although their quality in other respects is not to everyone's taste. Seedless grapes and oranges have been produced which pose a problem in propagation — but to this we shall return.

Important changes in seeds have improved the yield per acre, the size of the seed, the color of the stored food, the concentration of oil, vitamins and minerals, sugar or starch, and many other factors. Cotton has been carefully developed for the length of the fibers on its seeds, and even for its color. And to all this we may add that these improvements, which today give us products far superior to those enjoyed by our grandfathers, represent merely a beginning. New instruments and techniques are steadily increasing our control over the evolution of domesticated plants.

GENERAL QUALITIES OF DOMESTICATED PLANTS

Spectacular as some of the changes in the shape and form of plants have been, none can match in importance the hidden physiological changes that arise. Among these are changes in the content of sugar, fat, or starch, as well as higher yields of special compounds such as opium from poppy pods, cocaine from coca leaves, and rubber from the stem of the rubber tree. Even more important are the changes which enable the plant to grow under conditions where its ancestors would have failed. Chief among these are the abilities to resist disease and to grow under adverse climatic



Fig. 212. A stand of hybrid corn. In recent years hybridization experiments have increased the yield of this staple crop many fold.

conditions, such as the short growing seasons in the far north or far south.

A leading farm journal not long ago printed the statement that but for the work of Edgar S. McFadden, twenty-five million people who are eating today would be dead or dying of starvation. Although the value of McFadden's work is almost beyond computation, this man is by no means a unique benefactor. Rather, he represents a group of scientists whose work spells the difference between life and death for millions and yet is far too little known. No better example of man-made evolution can be presented than a brief review of McFadden's work in creating the wheat which he named "Hope." The story concerns the struggle against wheat stem rust, *Puccinia graminis*, a

fungus belonging to the Basidiomycetes. By destroying the tissue of the wheat stem this fungus causes the plant to break and fall before the grain ripens, so that a crop may be reduced to a tenth of its potential yield. In 1916, stem rust destroyed 200 million bushels of wheat in the United States and 100 million bushels in Canada. The effect of such losses on the world's food supply is obvious.

It was observed that of the many varieties and races of wheat, one, a variety of emmer wheat (*Triticum dicoccum*) called Yaroslav, appeared to be immune against rust. Because of its tough and fibrous nature, emmer could not be considered a substitute for bread wheat (*Triticum vulgare*). Although emmer is considered probably an ancestor of bread wheat, it has only 28 chromosomes, whereas bread wheat has 42. Hybridization under such circumstances is considered very difficult, but hybridization is what McFadden achieved. The first cross, begun in 1916, yielded a few poor seeds, one of which germinated and produced seed that was used for many further crosses. Such further crosses were necessary, for although the new wheat "Hope," produced in 1924, was resistant to stem rust, leaf rust, and five other major wheat diseases, it was susceptible to spring frosts and produced low yields. By building upon the work of McFadden, other plant breeders finally overcame these defects. It is estimated that today the progeny of McFadden's original seedling cover some fifteen million acres in North America, and that "Hope" derivatives saved \$135 million in the Dakotas and Minnesota in 1944 alone.

This story relates but a small part of the tremendous struggle for survival which man, like every other creature, must unceasingly wage. For no less than thirty-seven specialized races of wheat rust, each but slightly different physiologically from the others, are known to attack wheat. A new mutation in one of these may at any time nullify the resistance of the newly developed wheat. Indeed, this appears to have happened already and the work to produce "Hope" wheat must be done again.

A similar problem has faced the growers of

another cereal grain, oats. For many years various strains of a variety named Victoria had been widely planted and were considered the standard strain, when a new disease, *Helminthosporium*, a leaf blight, caused by a fungus of that name, began to make serious inroads on oat plantings. Today a new variety, Clinton, has been substituted for the various Victoria strains because of its resistance to this blight. However, Clinton oats have unfortunately proved susceptible to Race 45 of a leaf rust, and this, although not at present considered a serious threat, may become a major problem because of the great acreage of Clinton oats now grown. Thus this new successor of the Victoria strains may in turn require a successor. None is yet available, for the present varieties of oats resistant to Race 45 leaf rust are low yielders. The Department of Agriculture estimates that it will be at least three years before satisfactory Clinton substitutes can be developed.

The story of wheat and oats has been duplicated for many other crops raised by man. When asters appeared to be doomed by wilt diseases, new resistant varieties were found. Man has discovered a spectacular short cut in new gene-combinations in hybridization—that is, in combining traits of unrelated strains, notably in hybrid corn (Fig. 212). Tomato blight, caused by a downy mildew, has become more severe as plantings have increased. Today only sprays can check this disease, but the future will probably bring resistant varieties.

Not only has the plant breeder bestowed vast benefits on man by establishing disease-resistant varieties and increasing yield, but he has also been successful in selecting new races of plants with gene combinations that adapt them to climates differing from that in which they originally thrived. The northern limit to which wheat can be successfully grown has been pushed farther north during the past fifty years, as has that for corn, vegetables, and many varieties of flowers. Conversely, plants that have been developed for maximum production in certain special types of climate have lost their ability to thrive in other parts of the world.

Thus the fine varieties of corn that grow to such imposing size in the corn belt have proved miserable failures in competition with native varieties in many sections of South America. More and more strains of plants are becoming specialized for resistance to certain local diseases and for specific climates. Man-made evolution is nowhere more evident than in the field of plant breeding.

The adaptability of plants is at once man's despair and his hope, for because of it he must constantly fear new mutant blights, yet this very quality enables him to develop new resistant varieties.

NON-HEREDITARY METHODS OF PLANT IMPROVEMENT

In his struggle to improve plants and thereby to make possible a pleasanter life for himself, man is not limited to mutations and chromosome recombinations. In fact, more immediate progress has been made by other methods. These are of two main kinds, various forms of grafting, and the use of natural and synthetic hormones. Of these two, grafting is by far the older method, but the use of hormones begins to promise untold benefits.

Grafting

Grafting consists in causing a part of one plant to grow upon another. At first sight, this may not seem to offer great advantages. In order to grow well one upon the other, plants must be rather closely related. Thus tomato shoots have been grafted upon potato stocks, and while such a graft will produce tomatoes on the upper portion of the shoot and potatoes on the lower, there is no actual gain, for the available leaf surface produces only so much food material, and this will have to be shared between the two crops. But there are innumerable cases in which great advantages are gained. We can consider only a few of them.

One important use of grafting is for propagation. Many forms of fruit and flowers are heterozygous in their chromosome make-up. That is, their characteristics are due to the

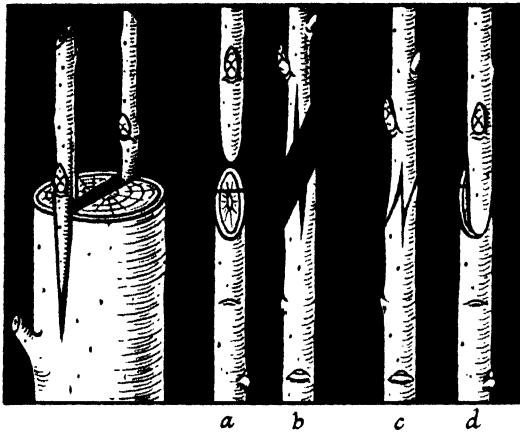


Fig. 213. Some forms of grafting. Left: A cleft graft ready for waxing. Two cions from desirable stock have been inserted into cleft stump so that cambium meets cambium. Right: whip graft; a and b, cion above, stock below, ready for insertion; c and d, cion inserted.

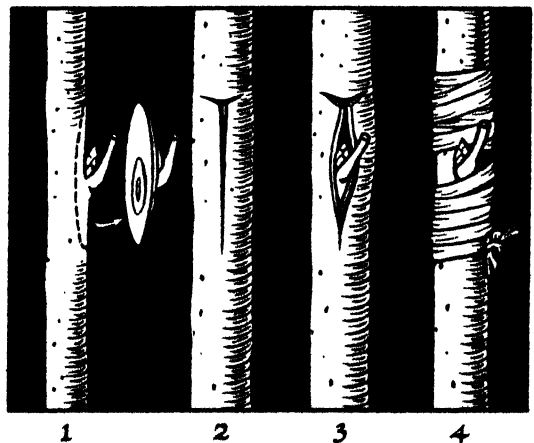
joint action of different chromosomes contributed by the two parents and acting on the same characteristic. Thus a red flower crossed with a white one may produce pink, but two pinks bred together may in turn produce reds and whites, since their pinkness is due to the joint action of the genes for red and white. Many desirable characteristics of flowers and fruits are due to such combined gene action, but it is impossible to guarantee the nature of the offspring. Furthermore, where many different varieties of fruit are grown close together, it is never possible to predict where the pollen that pollinates a given blossom will come from. For this reason, seed from a McIntosh apple growing on a McIntosh apple tree is not likely to produce seedlings that will again bear McIntosh apples. They are more likely to bear apples different from any others that were ever produced. Some may be better; most will probably be poorer. If an apple grower desires to have an orchard bearing McIntosh apples, he must propagate his trees vegetatively, that is, asexually. This is accomplished by grafting a twig from a McIntosh apple tree onto the root of some other apple seedling (Fig. 213).

A similar method is *budding*, that is, inserting a bud of the desired variety under a slit in

the bark of a seedling stem (Fig. 214). When this is done, all growth above the graft is removed, either at the time or later, and the entire tree or shrub develops from the cells of the bud by mitotic divisions. In these forms of propagation, the entire bearing portion of the tree will of course contain the genes of the cion (grafted portion) and will bear the fruit characteristic of the plant or flower from which it was taken. Only in this manner can a new variety of fruit be propagated at once, or a new hybrid rose perpetuated. There is no other way of propagating a seedless grape or orange.

Grafting may also be used to combine characteristics from several different plants in one. Not that a grapefruit, for example, may be produced by grafting an orange on a lemon root; for the root does little more than supply the shoot with water and salts. But roots are as susceptible to pests as other parts of the plant. Thus in some varieties of European grapes which yield superb fruit, roots were attacked by the root louse (*Phylloxera*) inadvertently brought to the continent from North America. Control measures were impracticable, and the grape industry of Europe was threatened. American varieties, however, were relatively immune to the attacks of this native pest, for natural selection, presumably, had made them so. Thus by grafting shoots of the European

Fig. 214. Steps in budding. 1. Budstick and bud. 2. Stock with T-shaped incision in bark. 3. Stock with bud inserted. 4. Completed graft tied with raffia.



varieties onto roots of American stock, the resistance of the one was combined with the quality of the other.

Bearing quality in fruit trees has been enhanced by means of grafting desirable but tender varieties onto hardier and more vigorous roots. In some cases, the vigorous root of one variety is grafted to the hardy stem of another, upon which in turn there is grafted the producing part of a third variety that yields superior fruit. So that they will grow in the dry Mediterranean regions, apricots are grafted onto almond stock. Since, however, the apricot does not easily form a union with the almond, a peach trunk, which unites well with both, is grafted between the two.

For the small home owner, dwarf fruit trees bearing normal-sized fruit are offered by many nurseries. They are produced by grafting a cion from a standard tree onto a slower-growing root stock, as pear on quince. The dwarfing effect ends if the cion develops its own root system, as often happens when the grafted tree is planted too deep.

These are but a few of the many improvements that can be achieved by various forms of grafting. In a sense they are makeshift measures, for certainly it would be much more desirable to obtain similar results in genetically pure stock that would breed true. Whether this will ever be achieved it is difficult to say.

Plant Hormones: Natural and Synthetic

When man has failed to create plants with hereditary traits that he considers desirable, he has in recent times forced the behavior of plants into new channels by exposing them to those very chemical substances that normally control their behavior, but at times which best suit his own needs. It is now known that apples drop when they are ripe not because of the pull of the apple on its stem, but because hormones which are produced in the tissues cause a weakening of the stem. Naphthalene acetic acid applied to the apple tree at the proper time will postpone this weakening for several weeks, thus preventing economic loss through injury to dropped fruit. In order to do this, it is not

necessary to paint the individual apple stems but simply to spray the entire tree.

Other substances, also used as sprays, hasten the shedding of leaves in the cotton plant, so that mechanical pickers may gather the fiber without picking leaves. It is also possible to eliminate or to prolong the period of dormancy which many plants experience after reaching maturity. Periods of dormancy are an important natural adaptation to the vagaries of the weather, for otherwise a warm spell in the fall might cause trees to bud and bulbs to sprout with disastrous results; or plants might not bud at the right time in the spring. Impatient man sometimes wishes to alter this rhythm. He wishes spring flowers in December, and now he can obtain them by exposing plants to suitable gases, thus eliminating the dormant period. Or he wishes to keep his potatoes, turnips, and carrots from sprouting in storage toward the end of the winter, as they usually will. Less than one gram of certain new hormone-like chemicals will prevent sprouting in a bushel of potatoes for an entire year.

The ability to produce roots from cuttings is found in many if not most plants, but in some the ability is rather feeble. Application of auxins (indole butyric acid) will tremendously hasten the process of root formation, thus greatly simplifying the process of vegetative propagation.

The greatest promise in man's control over plants appears in the form of the new hormone-type selective weed killers. Some of these kill broad-leaved plants but not grasses, and are thus almost ideal in keeping lawns free of weeds. Unfortunately, however, they also kill clover. Others kill crab grass but do not harm the better lawn grasses. It is now possible to spray a carrot field with a weed killer that will destroy practically all weeds but leave the carrots unscathed. Where scores of boys had to inch their way through acres of carrot plants and weed them by hand, we now find a sprayer eliminating all weeds by going once over the field. One effective weed killer, 2-4D, achieves its destructive action by unbalancing the rate of growth in different tissues of the leaf and stem, producing

peculiar malformations and finally death. Increased control over plants by agents such as these may hasten the day when weeds will be as rare in civilized regions as are wolves and mountain-lions today. But like all potential blessings which science bestows on man, these may be turned against him with devastating effect in warfare.

Potential Methods of Plant Improvement

A reasonably sound basic knowledge of the science of genetics is necessary for a full understanding of plant improvement through heredity. This topic has been reserved for a later chapter. Here it will be sufficient to recall that, with few exceptions, any hereditary change must come through a change in the genes, and that under normal conditions, such changes arise spontaneously and are called mutations. It should also be remembered that mutations are relatively rare and that they are more often harmful than not. It has been man's habit to watch for new mutations in domestic animals and plants and to perpetuate those he desires by judicious breeding. Similarly, desirable qualities in different species have been combined in new and better strains by combining the desirable genes of each, while rejecting those strains in which undesirable genes were in evidence.

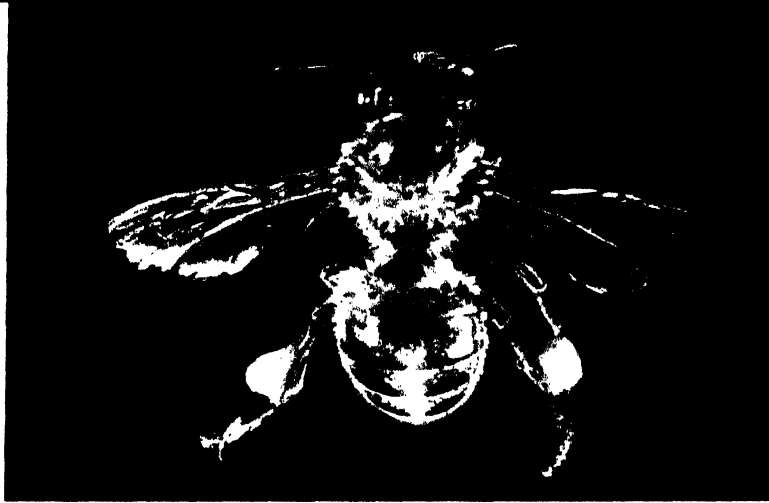
Until rather recent times, this was the extent

of man's power over the destinies of plants. He could select favorable mutations from among those which appeared from time to time, he could recombine these variants with other strains already available, and he could modify the environment to produce desirable changes. But he could not create new characteristics in the plant. In recent years, for the first time, man has discovered that he can induce mutations, both in plants and in animals. We have seen that through the use of various penetrating radiations it is possible to cause many times the normal number of mutations. But man's skill in creating changes must still be considered as being in a very primitive stage, for as yet he is unable to exert the slightest directive guidance over the changes he is creating, and, as we have seen most of the changes he produces are destructive. It is not impossible that the next, and perhaps final step, in man's effort to create and shape organisms according to his own desires, will be his ability to direct mutations, thus producing new genes by modifying old ones according to his preconceived specifications. Like so many powers, this could be made to yield great benefits or untold harm. Of one thing we may finally be certain; evolution will continue and plants in the future will be different from those of today, no matter whether evolution takes its own course or is guided by man-made selection.

PART FIVE

THE RISE OF ANIMAL LIFE





Among the invertebrates — animals without backbones — few show more complex behavior or more delicate adjustment to environment than the honeybee. This worker, wings frayed, and laden with pollen, is probably on his way back to the hive.

The First Animals: Protozoa

From Plant to Animal

As all living creatures have certain qualities in common, so all animals share certain characteristics which differentiate them from plants. Most obviously, animals move, and most plants do not. In general, plants show less distinct differentiation into organs and organ systems than animals do. And animal metabolism (see Chapter 4) differs from that of plants in that animals are less able to synthesize all the organic compounds of which they are composed, while plants in general can and do. Animals live by introducing into their cells, or bodies, the substance of other organisms. They eat. In this manner they differ not only from the autotrophic plants but from the heterotrophic ones as well. For while heterotrophs also require organic compounds, these may be simpler and more limited, and are usually obtained in solution from the products of bacterial disintegration.

On the whole, these differences are clear-cut, yet no sharp lines can be drawn between the kinds of living things, and many organisms possess characteristics of both animals and plants. Indeed, the further we go down the scale of life, the oftener we find this to be true, until some of the most primitive organisms, such as the simpler flagellates, can equally well be called either animals or plants.

Heterotrophs, living upon the first spontaneously produced organic molecules, may well have been the first type of living organism (see Chapter 3), and it is from these that animals and plants both were probably derived. The nature of animal metabolism precludes the possibility that animals came first; hence they, like the green plants, were probably evolved

from heterotrophic forms. It is among the flagellates, some of which are still heterotrophic, that we find the most primitive green plants, and perhaps the most primitive animals too. Among the flagellates of today, we see conservative descendants of those organisms from which two basic ways of living, those of the green plant and the animal, respectively, originally branched off.

Protozoa: The Simplest Animals

Among the *Protozoa*, or "first animals," are the simplest of all animal forms in one important respect, namely, that they are composed of but a single cell — a mass of protoplasm within a single cell membrane and usually with a single nucleus. But modern protozoans, like everything else alive today, are products of evolution, and mutation and selection have produced among them certain types which surpass in complexity any of the individual cells of the metazoan animal.

About 15,000 to 20,000 species of the *Protozoa* have been identified, though doubtless many still remain undiscovered. The *Protozoa* range widely in size — from a length of 3μ for *Leishmania*, a flagellate, to 5000μ for the rhizopod *Chaos chaos*; yet even the largest protozoans are minute. As is the way of living things, they display all conceivable shapes and patterns, sharing with each other as protozoans only their common animal characteristics, and the special fact that generally each consists of but one unit of protoplasm with its governing nucleus. Many protozoans are free-living, but great numbers of them are parasites, and there is hardly a larger multicellular animal that does not harbor some more or less parasitic proto-

zoan form. Thus the Protozoa are important not only as representatives of the first animal organisms, but also as cogs in the ecological interrelationships of life. As parasites, they affect the health and welfare of man and of those organisms of which he makes use.

PROTOZOA AND THE ANIMAL FUNCTIONS

Within its single cell, a protozoan performs all the basic animal functions which in higher animals are carried on by a variety of organs and organ systems. If we are inclined to express amazement that a microscopic droplet of protoplasm can perform the intricate chemical and physical activities entailed in the process of living, it may be well to remember that even though there is differentiation and specialization in the cells of the metazoan, such as man, each cell must still perform the basic operations of living, even as protozoans do. The fundamental activities performed by all animals, and in a variety of increasingly complex ways in the metazoan, must take place within the single cell of the protozoan. Let us see what these animal functions are.

First, unless an animal digests its food outside its body, as some protozoans do, it must ingest, that is, take the food into its own body in the form in which the food is found. Second, all free-living protozoans, and most other animals, must digest, that is, transform the organic matter they take in into a usable form. Then, since food ingested and digested does not at once find itself in all parts of the protoplasm, it is necessary to distribute the compounds throughout the organism. In the protozoans, streaming movements within the protoplasm, as well as diffusion, perform this function. The sum of all the chemical activities going on within the protoplasm is animal metabolism, which results in the utilization of the compounds absorbed. Since these processes produce soluble wastes, the animal excretes. In the protozoans, this function is performed by all parts of the cell. Undigested and indigestible material is then egested from the organism — in protozoans, usually by somewhat modified portions of the protoplasm. A process neces-

sary to metabolism is respiration, in animals the intake of oxygen and the giving off of carbon dioxide. In protozoans, and indeed in all animal cells, this takes place by the diffusion of the gases through the cell membrane between the protoplasm and the environment. All animals are capable of movement, which appears to be accomplished by more or less differentiated protoplasmic structures capable of periodic contraction. Animals also possess coordination, which in some protozoans appears to be a general and inherent function, while in others it is performed by highly differentiated regions of the protoplasm. Finally, all animals reproduce — protozoans, chiefly by mitosis.

In sum, the individual protozoan carries on all the functions performed by higher multicellular organisms, but on what has been termed a "protoplasmic level." The most highly evolved protozoans are therefore more complex than any single cell of a more complex animal, although as organisms they are usually less complex than even rather primitive metazoans. Protozoa are too small to permit much further differentiation than they already show, and their structure sets rigid limits to their size. It will be recalled that as a body increases in size, its surface area increases far more slowly than its volume, and it is through the surface that the exchanges of substances between protoplasm and environment take place. Furthermore, since the rate of diffusion remains constant, it follows that if an organism increases to twice its previous diameter, it will require twice as long for diffusing substances to reach the same concentration in the protoplasm. Evolution within the protozoan pattern is thus strictly limited. Yet in spite of that limitation, the protozoans are remarkably varied in complexity.

TWO REPRESENTATIVE PROTOZOA

The Amoeba: A Simple Protozoan

One of the best known of the Protozoa is the *Amoeba*, which, like all protozoans, is microscopic in size, though the largest ones may be just seen as white specks a fraction of the size

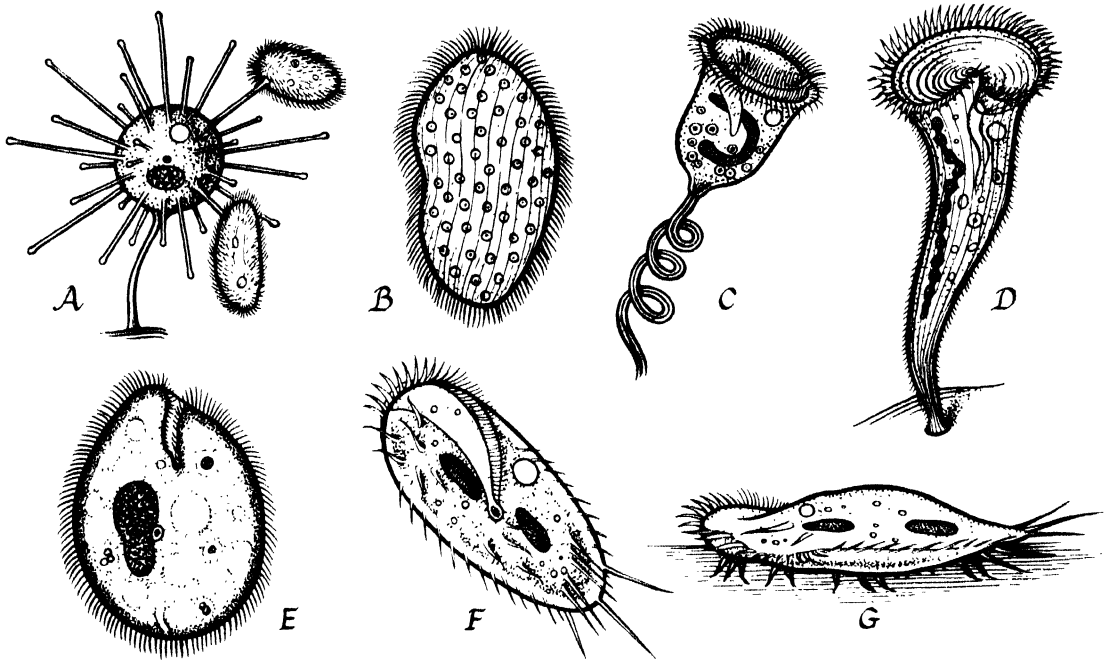


Fig. 216. Some representative ciliate protozoans. *A.* A suctorian, *Podophrya*, without cilia in the mature stage. The specimen shown is extracting the protoplasm of two captives with its siphon-like tentacles. *B.* The holotrich *Opalina ranarum*. *C.* A peritrich, *Vorticella*. *D.* A heterotrich, *Stentor polymorpha*. Note beaded nuclear chain. *E.* Another heterotrich, *Balantidium coli*, which inhabits the large intestine of the hog without producing any apparent ill effect. In man it causes balantidial dysentery. *F* and *G.* The hypotrich *Stylonichia mytilus*. With a body that looks much like that of an insect, it has "legs" of fused cilia and runs about with great speed and dexterity.

of a period in print. The amoeba is justly famed, for it exhibits, as few other creatures can, the simple primitive character of protoplasm, stripped of all concealment and refinement. No one who has ever observed this animal through a microscope is likely to forget the experience.

We may obtain an amoeba in the sediment taken from the edge of a small pond. If we place a drop of water containing an amoeba on a slide, with the cover-glass supported on a small hair so that its weight will not crush the delicate creature, we may examine it for hours on end. Simple as this drop of jelly appears, we can for a long time continue to find in it new structures and processes that escaped us before. Viewed under low power, the amoeba may be easily distinguished from the surrounding debris of dead organic matter by its characteristic gray, granular structure, sharply de-

limited by the cell membrane. At first the amoeba may resemble a drop of inert jelly and may show little sign of life. This is its way of reacting to the shock of being transferred to an unnatural environment between two sheets of glass. Given a little time, however, it will once more begin to move. To one accustomed only to the conventional animals of the everyday world, the behavior and appearance of an amoeba must come as somewhat of a shock, for it has no definite shape, no fixed top or bottom, and no recognizable head or tail. Yet it moves about, takes in food, and reacts to its environment despite its lack of any visible sensory structures.

Under a microscope, this irregularly shaped animal is seen to consist of granular cytoplasm, within which are scattered various formed bodies (Fig. 217). These bodies are mostly spherical in shape and contain an assortment

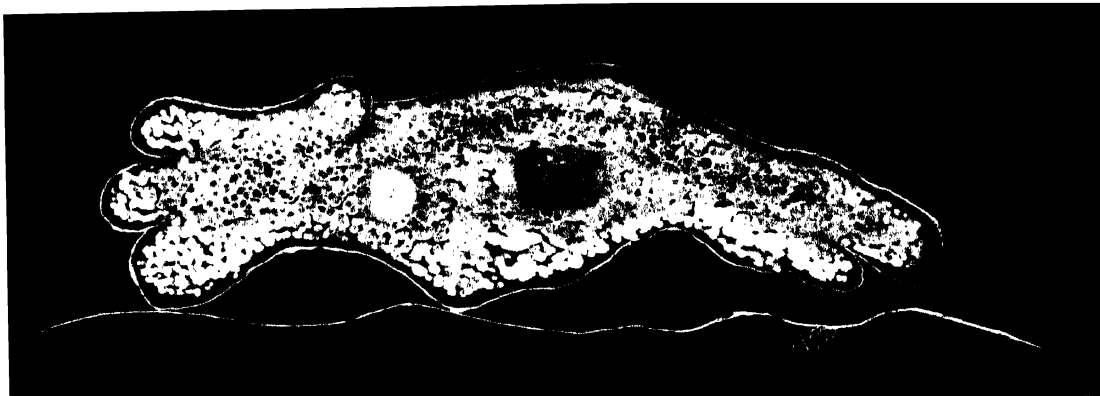


Fig. 217. An amoeba, a simple protozoan.

of structures that can be identified as whole organisms or fragments of organisms similar to those found in the water surrounding the animal. Sometimes smaller living protozoans, or even small metazoans, are found as captives, still struggling against their fate, inside these *food vacuoles*. In time the contents of the vacuoles will be digested and the soluble substances will then be absorbed into the cytoplasm through the membrane of the vacuole.

Another sphere within the amoeba is clear and transparent and appears to contain nothing at all, though actually it is filled with water. This vacuole pulses slowly, grows, then suddenly shrinks and disappears, while the cytoplasm surrounding it appears momentarily to be thrown into folds. Immediately afterwards the vacuole reappears, first as a minute white speck, which then once more expands and disappears again. This is the *contractile vacuole*. It appears to serve the same function as a bilge pump in a ship — that is, to remove excess water that seeps in. The cell membrane of the amoeba, as of all cells, is semi-permeable, and more water enters the cell by osmosis than leaves it. Plant cells, which are surrounded by a tough cell wall, build up pressure within them until external and internal pressures are equalized. The amoeba, lacking such a cell wall, would eventually burst unless it had some mechanism whereby excess water could be removed. This theory concerning the function of the contractile vacuole is strengthened by the fact that parasitic protozoans and those living in salt water do not have contractile vac-

uoles. In these species diffusion into the cell is not greater than diffusion outward. Placed in fresh water, however, they will frequently develop such vacuoles.

Still another structure to be seen is not spherical like the others, for as it flows along in the streaming cytoplasm, it appears to change its shape from time to time, though close observation shows that it only appears to do so because it is an irregular body that turns over and over as it flows along. Actually, this structure is shaped somewhat like a doughnut, although the central hole does not break through. In most amoebas there is only one such structure, although in some, many may be present. This is the nucleus of the cell, the carrier of the genes and the producer of many of the enzymes which control the chemical activities within the cytoplasm. The genes and even the chromosomes are not easily visible in the living amoeba. The living nucleus appears quite transparent and empty.

In the cytoplasm there is incessant streaming of the many granules suspended in it. These range in size from the lower limit of visibility, even under the highest power of the microscope, to clearly outlined particles, some angular and apparently crystalline, others spherical and glistening like liquid droplets. None of these particles shows any active motion of their own. In fact, perhaps the most striking feature of the whole organism is that it moves and responds without any apparent organ or structure to achieve its movement. At one moment the cytoplasm streams toward one end,

while the cell membrane bulges out in front of it, forming a characteristic finger-like projection called a *pseudopod* or "false foot." The next moment the streaming may be reversed, or may branch off at an angle, flowing into a new bulge while the old pseudopod disappears without a trace. If we recall our previous experiment with a droplet of mercury in a solution of nitric acid (page 43), it would seem that these activities may be compared to physico-chemical changes in the cytoplasm and the membrane, though the latter are unimaginably more complex.

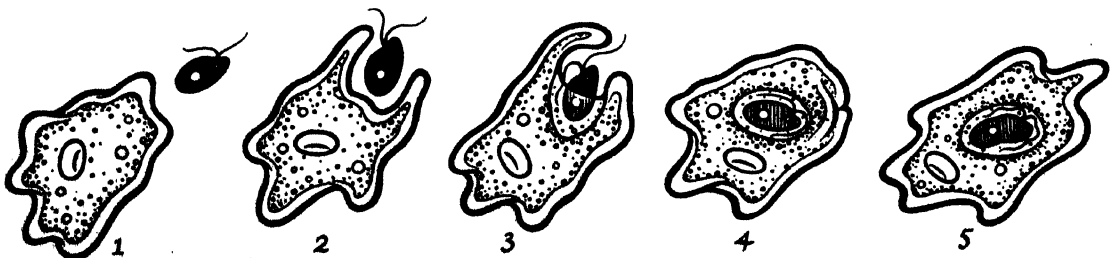
The newly forming pseudopod implies some sort of physico-chemical change in the cytoplasm. As the streaming granules pour into the pseudopod they appear to strike a non-liquid barrier some distance short of its actual tip, although the barrier is clear and contains no visible granules or other structures. In the trailing end of the amoeba this clear area becomes much reduced in extent and appears to be incorporated into the general cytoplasm again. This clear surface layer of the amoeba is the *hyaloplasm* or *ectoplasm* and appears to result from gelation where the protoplasm and the environment of the cell come in contact. But the gelation of the cytoplasm is not limited to the clear area just under the membrane. Cytoplasmic streaming is much more active well within the amoeba and becomes increasingly sluggish towards the surface, so that only a relatively narrow stream of cytoplasm actually flows. This streaming mass is referred to as the *plasmasol*.

The dynamic nature of the cell membrane becomes apparent when the amoeba ingests food (Fig. 218). Its pseudopods simply encircle the object and fuse around it. The portion of

the cell membrane surrounding the particle is then separated from the rest and becomes the membrane of the food vacuole. This, and the fact that a microscopic needle inserted through the cell membrane may be withdrawn without leaving a hole, sufficiently illustrate the living and dynamic nature of the membrane. After the digestive enzymes, secreted from the cytoplasm into the food vacuole, have transformed insoluble organic molecules into soluble, diffusible form, these compounds pass into the cytoplasm, there to be assimilated or broken down for the release of energy, while metabolic wastes are excreted through the cell membrane by diffusion also. Chemical indicators show that acid is secreted into the food vacuole, suggesting the probable presence of a protein-digesting enzyme like pepsin. Also by diffusion, oxygen enters the cell and carbon dioxide passes out of it in respiration.

The amoeba responds only to direct stimuli. In terms of what we know about its mechanism of movement, this simply implies that certain substances or certain forms of energy may either increase or decrease the viscosity or tension of parts of the cell membrane. Certain chemical substances cause the amoeba to flow towards them, others cause it to flow away, and it moves away from strong illumination. It may also have a memory of sorts, in proportion to its minute size. A second or third stimulus applied to it within an interval of some seconds will produce a response different from the first one, implying a carry-over effect from the first stimulus. But there is not much evidence of coordination beyond this. The amoeba appears to be so beautifully simple in its general scheme that it seems to operate "mechanically" and to require no dif-

Fig. 218. Amoeba ingesting a flagellate. The amoeba responds to the stimulus of an adjacent flagellate, encircles it with pseudopods, and closes over it. The flagellate within the drop of water in the food-vacuole will shortly be subjected to the action of digestive enzymes.



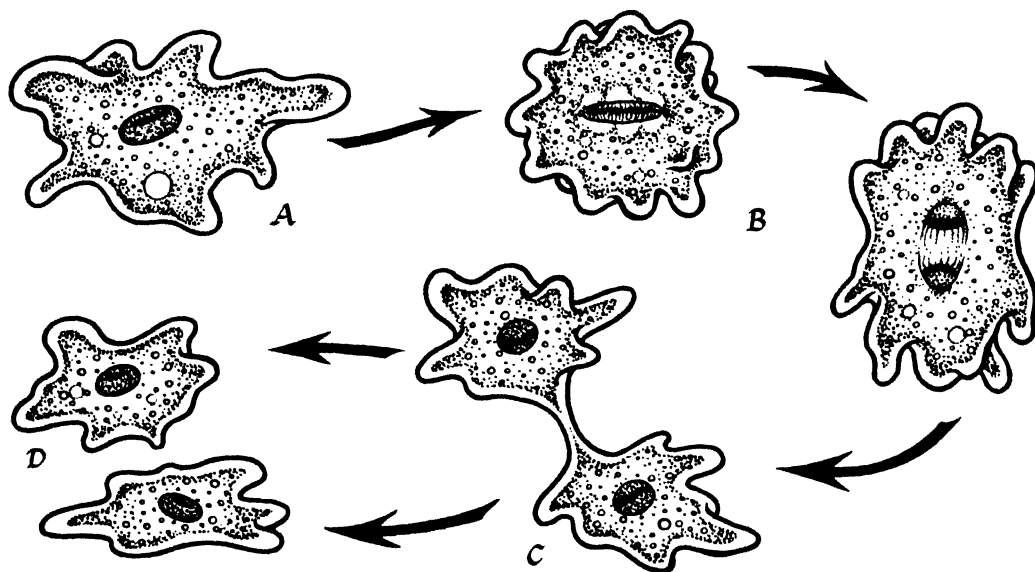


Fig. 219. Reproduction in an amoeba. *A.* Before division. *B.* Mitotic spindle and division of the nucleus. *C* and *D.* Two "daughter" cells are produced.

ferentiated or special coordinating mechanism.

The amoeba (Fig. 219), like most protozoans, ordinarily reproduces by mitosis and fission, though it may also reproduce by sporulation if conditions become unfavorable, as when its environment dries up. In the latter case the nucleus divides into many fragments, each one surrounded by a delimited mass of cytoplasm, while the whole mass is surrounded by an impervious, secreted cyst wall. Remoistened, the cyst will burst and discharge many small amoebas. In some amoebas, the internal fusion of two nuclei just previously produced within the cell by meiosis appears to be a sort of sexual act. The role of the nucleus in maintaining the anabolic processes of the amoeba was discussed on pages 83-84.

Simple and naked protoplasm, the amoeba carries out all the fundamental life activities of animals without benefit of special permanent organs to accomplish them.

Paramoecium: A Complex Protozoan

Still a single cell but structurally far more complex, the *Paramoecium* corresponds much more to our concept of an animal than the strangely amorphous amoeba. Being a pro-

tozoan, the paramoecium shares many characteristics with the amoeba, but it is probably as much higher in the evolutionary scale as the cat is higher than the earthworm. Paramoecia may be found in almost any sample of pond water or in any stagnant pool and may be cultured by the millions in an aquarium by adding organic matter which increases the bacterial population upon which paramoecium feeds. Under such conditions, white, cloudy streaks may form in layers in the water. These are dense masses of paramoecia.

A first attempt to observe the structure of a paramoecium under the microscope may be more exasperating than instructive, for the animals are incredibly energetic and swim very rapidly. But they may be slowed down or completely stopped in their headlong progress if placed on a slide with some methyl cellulose in thick solution. Having located a stationary paramoecium, we find that it is still not at rest. Rare indeed is the paramoecium that does not show active movement in some one of its many complex parts. The creature is elegantly streamlined (Fig. 220) and is thus able to glide through the water with a minimum of resistance. It differs from the amoeba most strik-

ingly in having a definite shape, in having many differentiated structures, called organelles, and in the precision and speed of its action. Thousands of small hair-like processes or cilia cover its outer skin or pellicle. The cilia, which are coordinated in their beat, are in constant motion and serve both to propel the animal through the water and to circulate the water around it, so as to bring suspended food particles to its mouth. The pellicle of the animalcule appears to be semi-rigid but elastic, for a paramoecium may change its shape in squeezing through a narrow opening. Immediately under the pellicle are numerous rod-shaped structures, the *trichocysts*, which under severe stimulation discharge a tangle of slender threads around the animal. These have been called weapons of defense, although this may be questioned, since discharge of the trichocysts is usually a prelude to death.

Within the pellicle the cytoplasm is clearly visible, and does not differ markedly from that of the amoeba, except that there is less active streaming. Moreover, the streaming is not so haphazard, for there appears to be a steady current that slowly revolves the cytoplasm around the center of the cell.

Food vacuoles are the most outstanding structures in the cytoplasm. If the paramoecium is well fed, many full ones may be seen crowded together in the posterior region of the cell, with more scattered ones toward the anterior end. New ones form constantly at the base of a funnel-like structure, the gullet, which opens to the outside in a spiral groove, the *oral groove*, that indents one side of the body. Two other striking structures are the contractile vacuoles. Located at either end of the cell, these look somewhat like diagrammatic daisies, although their shape is not constant, since they appear and disappear like the contractile vacuole in the amoeba and seem to serve the same function. Near the center of the cell is a larger, darker mass, the nucleus. Through the use of suitable dyes it can be seen that there are two nuclear structures, a relatively large *macronucleus*, and the much smaller *micronucleus*.

Refinements in the structure of the paramoe-



Fig. 220. The full complexity of a paramoecium cannot be shown even in a drawing this size, although the general complexity of its plan as compared to amoeba is apparent.

cium become more meaningful when studied in conjunction with their functions. Thus ingestion, which is far more complex and efficient than in the amoeba, involves numerous differentiated structures or organelles. The cilia lining the oral groove whip a constant stream of water into the gullet, where a membrane deflects the water outward again, while particles carried in this current, being heavier than the water, pass into the gullet. Here cilia glued together form a vibrating membrane which

propels the particles into a droplet of water — a newly forming food vacuole — at the base of the gullet. No such action would be possible without excellent coordination between the parts involved.

The paramoecium digests, absorbs, and assimilates its food much as the amoeba does. The food vacuoles slowly circle around the nucleus, gradually changing from acid to alkaline in reaction as they go. This can be seen by adding to the culture a drop of dye which turns red in an acid medium and yellow in an alkaline one, for when this is absorbed by the paramoecium, the food vacuoles in the posterior part of the cell turn red while those in the anterior part become yellow. This is of interest, since there is a similar sequence from acid to alkaline in the digestive tracts of higher animals and man. When the food vacuoles have made their circuit, they approach a spot in the pellicle of the cell called the anal pore. Here they burst through the pellicle, eliminating indigestible and insoluble substances.

Excretion is by diffusion, though the two contractile vacuoles may assist in the process. These are equipped with a number of small radiating canals which change in form as the vacuoles fill and empty, thus increasing the surface contact between the vacuoles and the cytoplasm and the speed of water removal.

While the amoeba simply “flows” along, the paramoecium has a distinct though simple system of movement, a multitude of microscopic oars, the cilia. When we consider that an entire paramoecium is no longer than the diameter of the period at the end of this sentence, it is difficult to imagine that each cilium can have its own driving mechanism. But it has even more than this, for each one beats in a certain rhythm. Just beneath the surface of the pellicle is a network of coordinating protoplasmic fibrils which probably correspond to nerves in higher animals (Fig. 221), for when similar fibrils in other protozoa are cut, the coordination of the involved cilia is lost.

Although the paramoecium possesses no visible sensory structures, it reacts to various stimuli. Thus it will seek out a favorable tem-

perature; it can orient itself with respect to an electric current in the water; it responds to various chemical stimuli about it; and it responds to mechanical stimuli. Thus, if a chemical gradient is established by placing a drop of water containing carbon dioxide in a dish of water with paramoecia in it, they will swim into the region of increased carbon dioxide concentration. And if they begin to swim out of it again, they will stop, reverse their course, and proceed at an angle back into the area of higher concentration. A converse reaction occurs when the concentration becomes too great. The reaction to mechanical stimuli is very similar. Since it cannot see, it swims along blindly in the characteristic corkscrew pattern caused by the twisting of its oral groove until it runs headlong into an obstruction. Immediately, it reverses the beating of its cilia, backs up a length or two, turning 30° – 45° away from its previous course, and darts ahead again.

The paramoecium does not show any great discrimination in the particles it ingests. Indeed, if we add some suspended carbon particles to its water, it sweeps these into its food vacuoles just as readily as digestible bacteria. Gorged to excess with such useless ballast, however, it may at length show “reluctance” to ingest any more of the same.

The paramoecium usually reproduces by mitosis and fission, but it may also reproduce sexually (Fig. 222). This latter process shows considerable evolutionary progress beyond the simple fusion of two cells, previously described among the flagellates of the plant kingdom. (1). Two paramoecia come together as if about to fuse, but merely establish contact through their

Fig. 221. Segment of the pellicle of a paramoecium. To each projecting cilium a coordinating fiber is attached.

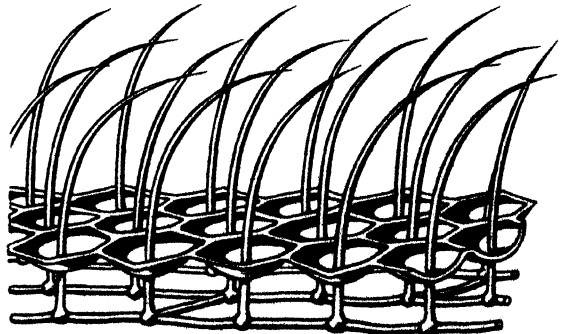




Fig. 222. Sexual reproduction in paramoecia. 1. Macronuclei degenerating; micronuclei in first meiotic division. 2. Completion of second meiotic division; 4 micronuclei in each. 3. Three degenerating micronuclei in each; fourth has again divided. 4. Migratory nuclei uniting with stationary ones.

oral grooves. (2). In each individual, the micronucleus then undergoes two successive divisions constituting meiosis, thus producing four haploid nuclei from the original diploid one. (3). Three of these degenerate while the fourth divides once more, thus producing two genetically identical micronuclei in each animal. (4). Sometimes this division results in nuclei of slightly unequal size, in which case the smaller nucleus of each cell now migrates across the protoplasmic bridge between the two paramoecia, which thus exchange "male" nuclei. It is noteworthy that only the two nuclei participate and not the entire cells. Each male nucleus now fuses with the non-migrating "female" nucleus of the other cell, and the two paramoecia separate.

This is the end of conjugation. Two cells started it and two cells remain at the end of the process. Further multiplication of the two paramoecia is essentially mitotic. The advantages of the sexual phase seem to be those gained by any organism that reproduces sexually. Hereditary strains are mixed, variability is increased, and the chances of survival for the species, if not for the individual, are enhanced. Paramoecia have been kept from conjugating for thousands of generation without apparent loss in vigor, but this does not mean a total absence of sexual reproduction in these strains. For a single paramoecium can,

like the amoeba described earlier, produce haploid nuclei by meiosis and then undergo a self-fertilization by the fusion of two such nuclei. In some forms several physiologically different types have been observed. These variants appear to produce hormone-like substances which attract some types of their species while repelling others. As many as eight of these "sexes" have been observed in a single variety of paramoecium. Such a device would clearly increase variability in the species, by promoting the mating of animals of different strains. The paramoecium is indeed a vastly more complex creature than the amoeba.

VARIETY AMONG PROTOZOA

The Flagellates

The amoeba and paramoecium are but two of an amazing variety in form, shape, size, and mode of life of the Protozoa, which range from near-plants to distinct animals. Yet the many thousands of species all fall into four main classes. Of these the most primitive are the *Flagellata*, which have one or more whip-like processes by which they propel themselves through the water. As we have seen, since some of these contain chlorophyll, they may almost equally well be considered plants, and it was such forms which seem to have given

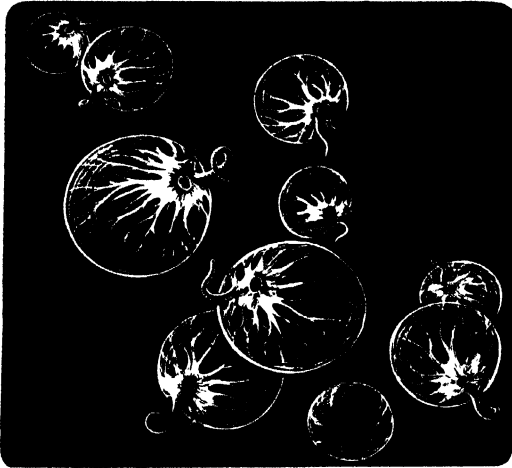


Fig. 223. The dinoflagellate *Noctiluca scintillans* causes brilliant "phosphorescence" in the ocean.

rise to the algae. Hence the flagellates may well be considered as a point of departure for both the world of plants and the world of animals. Indeed, they show almost every form of nutrition, ranging from the clear-cut extremes characteristic of plant and animal to the heterotrophic and the parasitic; and some may even have the capacity for many different forms of nutrition, depending on their environment. Also the flagellates are first to show a differentiation between germ and somatic cells and the appearance of "natural" death. In *Pleodorina* and *Volvox* we saw the first colonial forms on their way to becoming multicellular organisms, and we saw the destruction of the parent colony when the new one burst free of it (page 178).

Quite aside from their affiliations with both animal and plant worlds, the flagellates are an extremely varied and interesting group. Remarkable for its ability to produce animal light or luminescence is the dinoflagellate *Noctiluca scintillans* (meaning literally, "scintillating night-light"), which gives off much of the "phosphorescence" often seen in the ocean during summer nights (Fig. 223). Protozoa of another group, the *Choanoflagellates*, are holozoic in nutrition and have, around the base of their flagella, a peculiar funnel-like collar which

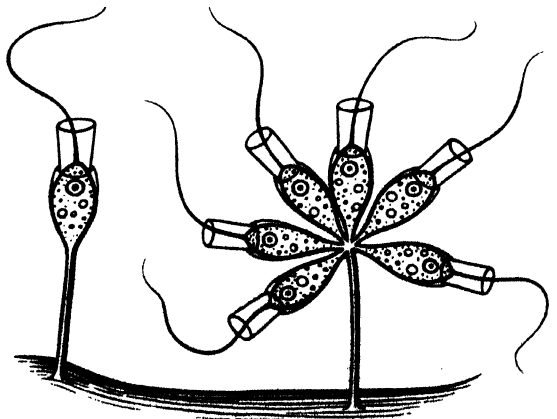
assists in the ingestion of food (Fig. 224). Later we shall find similar cells in the sponge. Many flagellates are disease producers. Living within the tissues or fluids of animals and man, they produce toxins or destroy tissues. *Trypanosoma gambiense*, the organism transmitted by the dreaded tsetse fly, is the cause of African sleeping sickness, while other varieties cause intestinal disturbances, destruction of blood cells, and certain forms of boils. As a thought-provoking evolutionary sidelight, it may be noted that, as with many bacterial diseases, native animals indigenous to an environment in which protozoan parasites are found frequently harbor these parasites without suffering great damage, while organisms not selected by ancestral exposure to such parasites frequently succumb. Thus it is said that in certain regions most wild game is infected with trypanosomes and yet remains apparently healthy.

Reproduction in the flagellates is usually by longitudinal fission, although it may be sexual — and sometimes highly specialized, as in *Volvox*.

The Rhizopods

The second large group of protozoans is the class *Rhizopoda* (Gr. *rhiza* = root + *podos* = foot), single-celled creatures which usually have no stable body configuration but form pseudopods by thrusting a portion of their protoplasm in one direction or another. The amoeba belongs here. All rhizopods ingest food like the

Fig. 224. The choanoflagellate *Codosiga*. These cells, remarkably similar to some characteristic of sponges, form colonies when a cell which has divided fails to separate completely from its twin.



amoeba, but they may differ widely in the form of their pseudopods and in general appearance. Some are free-living, holozoic animals like the amoeba, while others are saprophytic or parasitic. Because of the wastes they produce, some parasitic amoebas cause distressing symptoms in their hosts. Thus *Endamoeba histolytica* is the cause of the often deadly amoebic dysentery in man. Others regularly live in the intestinal tracts of various animals and appear to have no ill effect on the host. These are not parasites, but *commensals* — literally, “those who eat at the same table” — and some may even be symbiotic.

One group of this class, the order *Foraminifera* (Lat. *foramen* = perforation) (Fig. 225) is characterized by the possession of a calcareous shell, coiled like a snail's, which the animals build around themselves. This shell is usually perforated by innumerable tiny holes through each of which a slender, branched pseudopod extends. Particles of organic matter are engulfed and digested within these pseudopods. Foraminiferans are usually sessile — that is, attached to a substrate — rather than motile, and may be found clinging to seaweed. They are found only in salt water, and their skeletons form a large portion of the ocean-bottom ooze. Great chalk deposits, formed in past geological eras, consist largely of these skeletons. The magnitude of these deposits is shown by the fact that England alone produces about five million tons of chalk annually.

Still another order of relatively small rhizopods is the *Heliozoa* (Gr. *helios* = sun), which

Fig. 225. A living foraminiferan. The delicate, threadlike pseudopodia are barely visible.

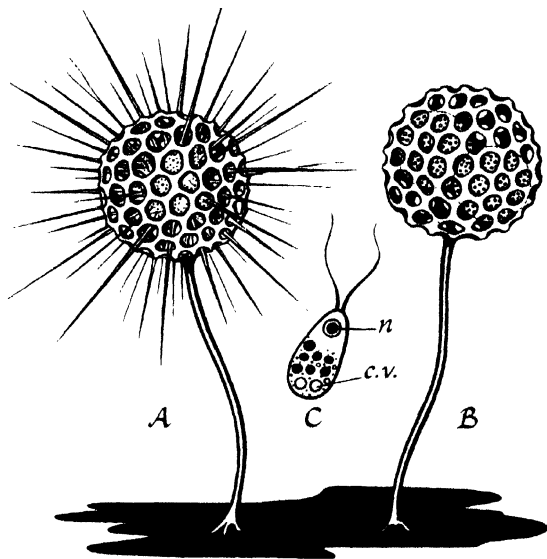
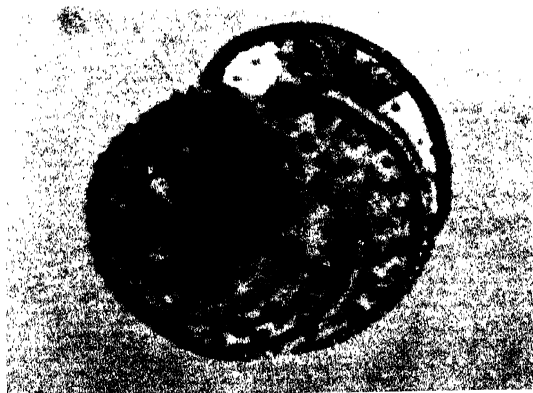


Fig. 226. A heliozoan, *Clathrulina elegans*. A. An individual with pseudopods extended through its skeletal apertures. B. An individual with pseudopods withdrawn and cell divided into two cysts. C. Zoospore with two flagella; n, nucleus; cv, contractile vacuole.

under the microscope look like miniature suns (Fig. 226). Many of these fresh-water animalcules also produce skeletons, though of a siliceous material. The protoplasm forms a sticky film over the radiating needles of the skeleton, and engulfs and digests the food particles wherever they stick. Various complex forms of sexual reproduction are found in this group, involving in some individuals a fusion of gametes produced within the same cyst, with no opportunity for the crossing of different strains.

The most varied and highly organized of the rhizopods are the marine *Radiolaria*. Producers of almost indestructible siliceous skeletons, often of great beauty and endlessly varied in pattern (Fig. 227), their remains form the principal constituent of millions of square miles of the Pacific and Indian Ocean bottoms. So durable are their glass-like microscopic skeletons that many of them have endured since late Proterozoic times, over 500 million years ago. They are indeed among the first signs of life on earth, and the flint-like masses which their consolidated skeletons produce are the oldest fossil-bearing rocks. But perhaps no less re-

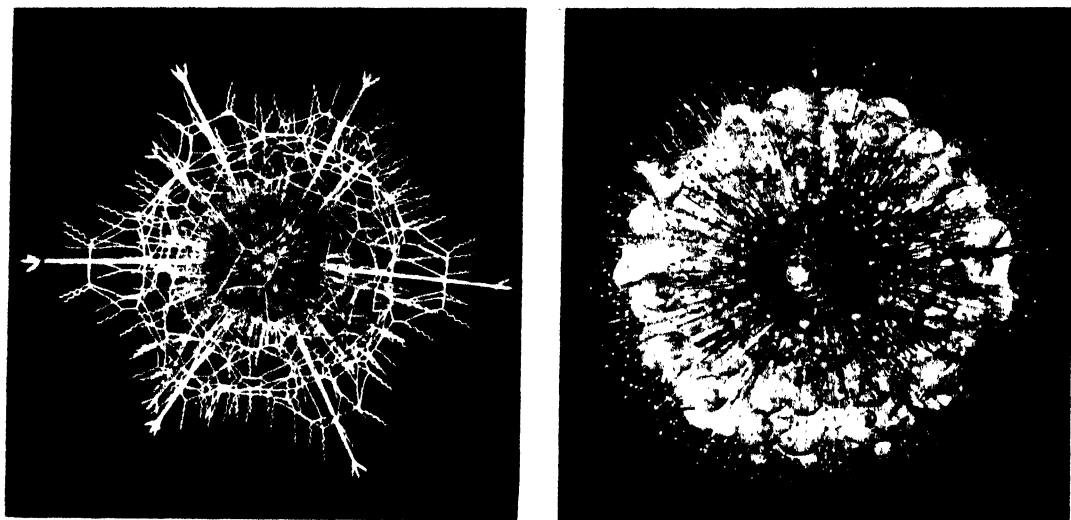


Fig. 227. Glass models of radiolarian skeletons, *Lychnosphaera regina* (left) and *Trypanosphaera regina*. Forming a veritable lacework of glass, these siliceous skeletons appear in almost unlimited varieties.

markable than their antiquity is the fact that they were then much as they are now, judging by their shells, and evolution appears to have touched them but lightly.

The tendency to form colonies — a prerequisite to metazoan evolution — is apparent in this group as in the choanoflagellates. Thus in the radiolarian *Collozoum inerme*, many individuals eventually come to occupy a common, expanded, gelatinous capsule. The separate individuals are united by a protoplasmic net which produces communal pseudopods at the surface of the capsule. *Collozoum* may also reproduce by means of zoospores. Hundreds or even thousands of daughter nuclei, each surrounded by a bit of the cytoplasm, are formed within a single capsule. These multitudes of cells gradually assume a kidney shape, develop two flagella, and begin to swim actively about within the membrane of the capsule. Eventually their tumultuous activity bursts the capsule and they are liberated. This recurrent return to flagellate reproductive forms is of considerable interest.

The Sporozoans

The third main group of protozoans, the class *Sporozoa* (Gr. *spora* = seed), consists of para-

sites without locomotor structures or ingestive mechanisms. They are interesting because of their complex reproductive cycles and important because of the diseases they cause. *Plasmodium*, for instance, is the cause of malaria, thought to create more sickness than any other disease that affects man. Directly — or indirectly, through its debilitating effect — about two million deaths annually are attributed to malaria in India alone, out of a possible one hundred million cases. Several million cases occur in the United States annually. There are four different species of this parasite, though *Plasmodium vivax*, cause of tertian malaria, is the most common in the United States.

Plasmodium vivax enters the blood stream of man in the saliva of a mosquito as it bites (Fig. 228). At this stage, the plasmodium is a small amoeboid cell which at once attacks and enters a red blood cell, where it grows and divides, producing many spores similar to the one that caused the infection. Reproduction is rapid, and a new crop of spores is produced every forty-eight hours. The mature spores are released from numerous bursting blood cells all at the same time, pouring into the blood stream a large amount of toxin which is the cause of each new spell of chills and fever. The new

spores at once attack new red blood cells and the cycle is repeated. Since this occurs once every forty-eight hours, attacks occur every third day. Hence the name "tertian" malaria.

But not all the new spores resume the original cycle. Some develop into male and female gametocytes and remain in this form until an *Anopheles* mosquito taps the infected person for blood. The gametocytes are then ingested with the blood and pass into the stomach of the mosquito, where they develop into gametes. The larger female gametocytes develop directly into eggs, while the smaller male ones divide, each producing six or eight slender flagellated sperm cells. Fertilization results in an active zygote which burrows into the stomach wall of the mosquito to encyst. Within the *oocyst* thus formed, multiplication is resumed, until many *sporozoites* are produced. These are released into the body cavity of the mosquito, migrate to her salivary gland, and are ready to be injected into another human victim. Since both hosts are essential to the completion of the life cycle of the plasmodium, malaria can best be eliminated by eliminating the *Anopheles* mosquito. Quinine and a synthetic drug, atabrine, are used successfully in the treatment of this disease. A number of new

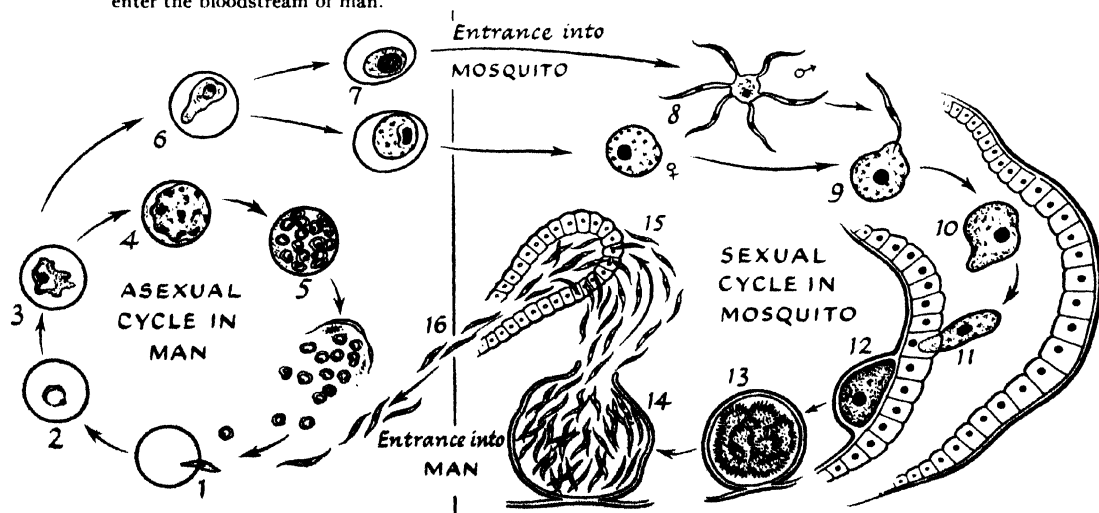
and even more effective drugs are now being tried out.

Certain sporozoans called *gregarines*, commonly found in insects, are also found in earthworms and unfortunately in oysters, where they cause serious economic loss. *Coccidia*, another member of this order, causes serious diseases in poultry and rabbits. *Babesia* causes Texas cattle fever. Pebrine, a disease of the silkworm caused by another sporozoan (*Nozema bombycis*), attacked the French and Italian silk industry in about 1850, and caused an estimated loss of £120 million during a period of thirteen years. It was in his successful work to learn the cause of this disease and how to overcome it that Louis Pasteur became convinced that germs are the cause of many diseases.

The Ciliates

Of all the protozoans, the ciliates show the highest variation in form and the greatest differentiation of internal structure. Although most ciliates are free-living, there are many commensals, symbionts, and parasites among them. Dozens of species have been found in the digestive tracts of horses and cows, though these usually appear to cause no damage or dis-

Fig. 228. Life cycle of *Plasmodium vivax*, the protozoan causing tertian malaria. 1-5. Entrance of sporozoite into red blood cell and proliferation therein. 6-7. Production of the gametocytes. 8. Their transformation into male and female gametes. 9-10. Fertilization and the zygote. 11. The zygote becomes actively amoeboid and burrows through the stomach wall. 12-14. Development of sporozoites in oocyst attached to outer layer of stomach wall of mosquito. 15. Sporozoites discharged from the oocyst wander through body fluids of mosquito to salivary glands. 16. Sporozoites carried in the saliva of the mosquito enter the bloodstream of man.



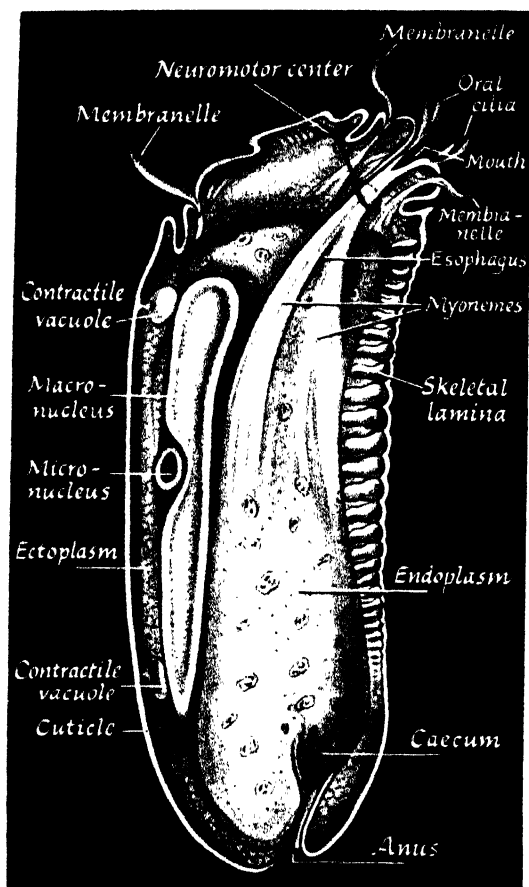


Fig. 229. *Diplodinium ecaudatum*, a ciliate inhabiting the stomachs of cattle, shows the extraordinary degree of intracellular differentiation of which protozoa are capable. There is even a highly differentiated neuromotor center.

comfort. The extraordinary complexity of this group is well illustrated by *Diplodinium ecaudatum*, which inhabits the stomachs of cattle (Fig. 229).

The ciliates differ surprisingly in the structure and distribution of their cilia. One type, the *holotrichs*, of which the paramoecium is a member, have more or less uniform, short cilia quite evenly distributed over their bodies. Among the members of this group are several parasites, including *Opalina ranarum*, which lives in the intestine of the frog, and *Balantidium coli*, which lives in the alimentary tracts of cattle (Fig. 216, p. 273). Those of a second type, the *heterotrichs*, have enlarged cilia, fused to form

membranelles surrounding the funnel-shaped opening to the gullet. The largest of the ciliates, *Stentor* (Fig. 216), is of this kind, and is a magnificent object under the microscope. Resembling a large, steel-blue trumpet, the stentor may attach itself to various supports by its tail-like process, or it may swim about freely. Perhaps the most amusing among the ciliates are the *hypotrichs*, many of which are odd bug-like animals with flattened bodies and quite large clumped cilia which have evolved into leg-like walking bristles. *Stylonichia mytilus*, one member of this group, can often be seen scurrying over the surface of aquatic plants on its rudimentary "legs."

Most pleasing in their delicate grace are some of the *peritrichs*, which have cilia only in a fringe around the funnel-like groove that leads to the gullet. One of these, *Vorticella* (Fig. 216), grows in dense clusters, each bell-shaped cell attached to a long thin stalk, by which it clings to its substrate. A thin, contractile strand extending the length of the stalk enables the vorticella to withdraw from doubtful stimuli with lightning speed. Indeed, the motion is too swift for the eye to follow. One moment an open, bell-shaped cell is extended at the end of its stalk, the cilia beating around its mouth like a motor-driven wheel. The next moment there is only a closed ball on a tightly curled stem clinging to the substrate.

The Suctorians

A final type of protozoan is grouped with the ciliates because, while its members do not have cilia as adults, they do have them in earlier developmental stages. These are the *Suctoria* (Fig. 216), so called because the adult forms have long tubular tentacles which the animal attaches to passing protozoa and through which they suck their prey dry.

In spite of the limitations imposed upon them by their microscopic size and by the absence of the clearly defined organs and organ systems found in higher animals, the Protozoa are an extremely varied group in almost every way — in size, shape, structure, habitat, and mode of life and reproduction. In fact, about all they

have in common is that they are minute, single-celled, and aquatic.

The Protozoa in Evolution

Evolution has shaped protozoans as it has all living organisms, and many of them are far from primitive. Although it is in this group that animal characteristics first appeared, most of the protozoans of today are distinctly divergent from the stream of evolution that led to the dominating metazoans; they are not merely primitive, backward, or conservative — they are different. To study the Protozoa as an early link in the evolution of animal life, it is necessary to select those few which have in evolution diverged least from the stream that presumably led to the higher animals.

To begin with, we can be quite certain that in the Protozoa was evolved the basic animal pattern of metabolism. They move about in search of food. They possess structures for motion, and sense organs, and coordinating mechanisms for directing their motion. They were the first animals to possess a kind of metabolism that makes it possible for them to commandeer the compounds and even the entire bodies of other organisms for their own uses. And having tapped such rich sources of fuel and structural material, they exhibit that ceaseless activity which a profligate use of

energy makes possible and which more than anything else characterizes animal life.

In their organelles, they exhibit the diverging adaptive character of all living organisms, but few of these evolutionary accomplishments have contributed directly to the evolution of the metazoans. The development of locomotor and sensory structures is a prerequisite to metazoan development, but clearly, the most significant step is to be found in the recurrent tendency of these animals to form groups of cells, as do some rhizopods, ciliates, and especially flagellates. Certain protozoans, in other words, became colonial organisms, and such cell groups had to appear before individual cells could specialize for limited specific functions, as in the metazoans. In such groups of cells there arises for the first time a phenomenon unquestioningly accepted as the heritage of all animals — physiological or “natural” death. This did not exist, however, until it was introduced by colonial aggregation, apparently as the necessary price of cellular differentiation.

Traces of protozoan ancestry are still evident in man's unicellular beginnings, the egg and the flagellated sperm, and in the colonial plan of his early embryonic stages. However different the separate links in the great chain of being, they yet reveal frequent and striking similarities.

Rise of the Metazoan Pattern: Sponges and Coelenterates

From Colonies to Metazoans

If it seems a long step from the individual cell to the colony, it is at least as long a one from the colony to the metazoan with truly differentiated tissues. And yet both processes were gradual and there were many intermediate stages along the way. We have seen that several types of protozoa independently evolved cell communities instead of living as separate, isolated individuals. The myxomycetes (pages 186-187), sometimes classed as rhizopods and sometimes as fungi, produce fused masses of previously independent cellular individuals. *Volvox*, a flagellate, is always an organized globular mass of individual cells, and though these are all alike except the germ cells, they no longer appear able to exist independently. In some ciliates numerous individuals, each similar to the single cell of a *Vorticella*, grow together on a single stalk. None of these groups can be called metazoan, since the cells within the communities generally maintain their independence and show no differentiation. In an organized colony such as *Volvox*, where there is a sharp distinction between germ and somatic cells, it is possible to call the colony an individual, although it is generally not so considered.

That the colonial pattern appeared repeatedly in different branches of the evolutionary tree is certainly no indication of its usefulness. But the fact that this pattern is to be found among organisms that still exist today indicates that it must offer some advantages in the struggle for survival. Once the colonial pattern had been evolved, it was almost certain that sooner or later mutations would appear which

would lead to differentiation and specialization within the colony. Under certain conditions, even the primitive beginnings of specialization seem to have offered advantages sufficient for survival, and among animals living today there are still many intermediate stages.

Metazoan Advantages and Disadvantages

Some of the advantages and disadvantages inherent in the metazoan pattern are self-evident and are much the same as those in plants. Increase in size makes the organism less vulnerable to attack. Differentiation and specialization make possible an increase in the efficiency of a cell for a particular function. In tracing the evolution of plants, we saw that full adaptation to land life would have been impossible without such differentiation. The chief disadvantages of multicellular construction are the difficulties faced by the individual cell in supplying its basic needs. Any cell within a cluster is surrounded by others with similar needs for oxygen, water, and food, and with similar wastes to dispose of; whereas every free-living cell is surrounded by water from which it can draw the things it needs and into which it can excrete its wastes. To put this differently, the colonial or multicellular organism, because of its increase in size, has suffered a change in surface-volume ratio, since as size increases, volume grows much faster than surface. Still another difficulty arises in the increased distances over which foods and wastes must be transported. In the one-celled organism substances have to travel, at an average, only half the diameter of the cell. But in the

multicellular organism, they often have to travel many thousand times this distance, from cell to cell, until they reach the innermost — or outermost — cells in the group. Without the introduction of special transportation systems, as well as special systems which in effect increase the relative surface, further evolution in multicellular organizations would be limited.

But these difficulties are overcome in several ways. A group of cells spread out in a thin sheet has many times the amount of surface it would have if arranged in a compact lump, just as a pile of wet sand will dry faster if spread thin, since more of it is exposed to the air. A multicellular organism, instead of developing into a solid mass of cells, could take the form of a thin sheet, perhaps folded or pleated to be less cumbersome. Many organisms have evolved in just such a manner. Also valuable are mechanisms whereby diffusion can be speeded up. This would ensue if the cells of the organism were bathed in a common body fluid which could be circulated by a mechanical means. This too has come about, and has been elaborated in many ways. All these things imply the specialization of certain cells in certain functions; and this also has happened, so that the metazoan gradually evolved out of the colony and special cells took on special tasks and special forms, until gradually there arose different kinds of tissues. In the three simplest metazoan groups, the sponges, the sea anemones and their relatives, and the comb jellies these developments are well under way.

THE SPONGES

The simplest and most primitive real metazoans are the sponges, phylum *Porifera* (*L. porus* = pore + *ferre* = to bear), which have at times been described as colonial flagellates. Probably originating from some form of colonial protozoan, and not closely related to any higher forms of life, the sponges are thought to be a divergent branch of evolution and a dead end. Nevertheless they are of great interest, since they show more clearly than any other animal forms those first important steps beyond colonial organization in the direction of the

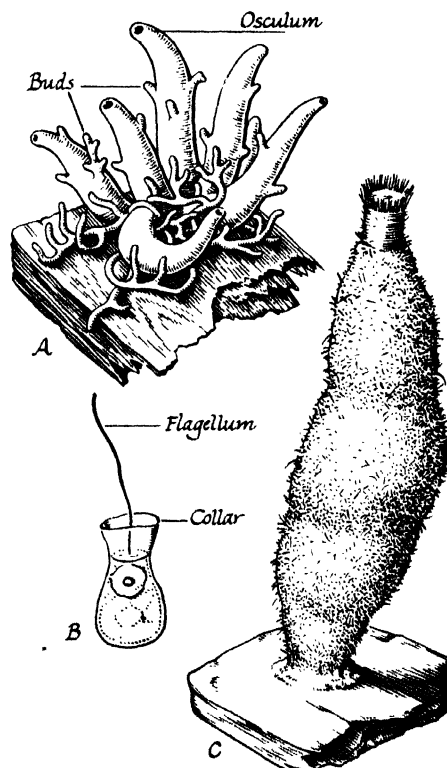
specialized and organized metazoan structure.

At first glance one might have some trouble in classifying sponges as animals of any sort. They live a completely sessile life on the floor of the ocean, sometimes several miles below the surface, and give no outward signs of motion. A live sponge does not much resemble the familiar sponge of commerce but looks rather like a piece of raw flesh somewhat the worse for prolonged submergence. Only close examination shows that there is any activity at all within the inert lump, but water may be seen to enter through countless pores on the surface of the creature and to emerge again through one or more exits. The animal nature of the sponge becomes apparent only when we observe its living tissue under the microscope.

Kinds of Sponges

According to the nature and complexity of their skeletal structure, sponges are of three main kinds. The simplest ones such as *Leucosolenia* (Fig. 230) and *Grantia*, are small shal-

Fig. 230. *Leucosolenia*. A. A colony. B. A collar cell. C. Single sponge.



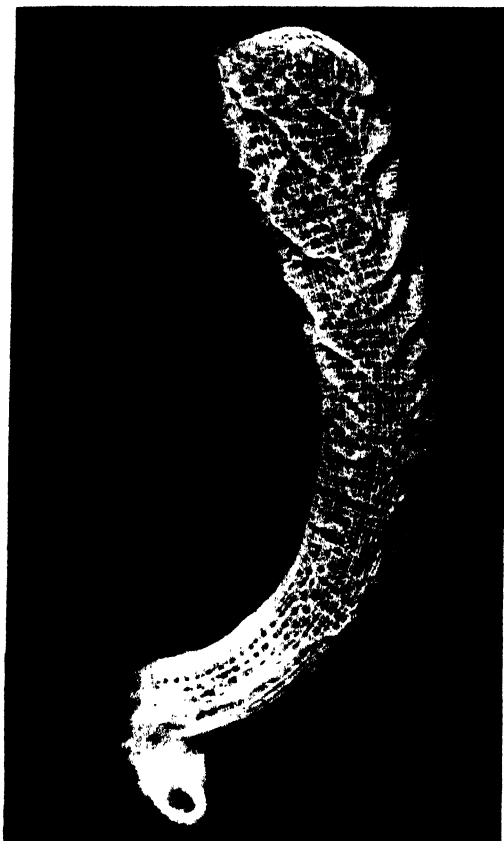


Fig. 231. *Euplectella* (Venus's Flower Basket). A glass sponge. Their dried skeletons, made of lacy siliceous spicules, are of great beauty. This sponge grows in deep waters off the coast of the Philippines.

low-water forms with a skeleton of very tiny calcareous or limy needles and spars, called spicules. Somewhat more complex than these are the so-called glass sponges, which have skeletons of siliceous spicules with three axes, and hence six rays. The skeletons of these creatures are lace-like and glassy, and some of them are of exquisite beauty, e.g., Venus's flower basket (Fig. 231). These are generally deep-sea forms. A third and still more complex group includes the horny sponge of commerce, the bath sponge. Derived from the glass sponges, these may have siliceous skeletons though not of the six-rayed configuration; or they may have skeletons of spongin, a flexible, fibrous substance; or of neither material. The group includes fresh-

water as well as marine forms, some of which attain considerable size (Fig. 234).

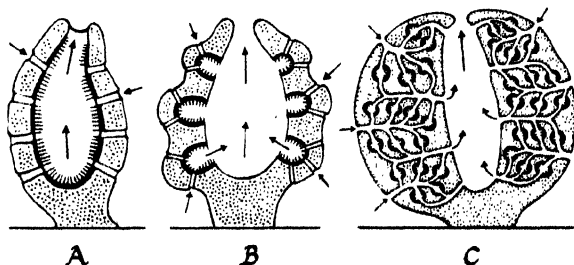
Organization in Sponges

Simple as they are, the sponges are far more complex than even the most advanced colonial organisms, for not only do they have clearly differentiated types of cells beyond the simple division between somatic and germ cells, but there are suggestions of organs and special areas within the body, and even, in a rudimentary form, the beginnings of distinct tissue layers.

The tiny ascon (Gr. *askos* = bag) type sponge, *Leucosolenia*, which looks quite unlike a typical commercial sponge, grows in clusters clinging to any firm surface. Sliced lengthwise, it is found to have a distinct though simple structure. It is actually a little hollow vase consisting of three layers of tissue (Fig. 232). The body is pierced by many small pores through which water is drawn into the interior cavity, to be pumped out again through the larger opening at the top. The outer tissue layer consists of flattened dermal cells, while the inner layer is a complete lining of collared flagellated cells strikingly similar to those of the choanoflagellates. In the space between these two layers is a third, varying in thickness in different sponges, and consisting largely of an inanimate jelly within which several kinds of cells — amoeboid or wandering cells and reproductive cells — are scattered. This is the *mesoglea* (Gr. *glea* = glue).

There are not many different kinds of cells in

Fig. 232. Section through three types of sponges. Increase in complexity mainly involves arrangement of cavities lined with collar cells and thickening of mesoglea. A. Ascon type, *Leucosolenia*. B. Sycon type, *Grantia*. C. Leucon type, *Spongilla*, *Euspongia*.



the sponge. There are the cover cells of the outer layer, some of which are special pore cells through which the incurrent pores pass. There are the amoeboid cells of the mesoglea, which take over various functions, such as digestion, transportation, or the manufacture of skeletal spicules. These cells may even be transformed into gametes or reproductive cells. Finally there are the collar cells of the inner layer (Fig. 233). And yet this is a notably higher degree of specialization than appears in colonial protozoans.

The structure of all sponges is essentially like this except for the amount of folding the tissues undergo. In the simplest ascon or "bag" sponges, there is relatively little folding, and the walls of the body are rather thin (Fig. 232). In sponges of the sycon type (Gr. *sykos* = fig), the inner surface is curled into folds and pockets and inasmuch as its area is thus considerably greater, the number of ingesting collar cells is greatly increased. Finally in sponges of the leucon type (Gr. *leukos* = white) there are

Fig. 233. Types of cells in sponges. 1. Dermal cells. 2. Mesenchyme cells. 3. Pore cell, which surrounds an incurrent pore. 4. Mesenchyme cell forming skeletal spicule. 5. Contractile cells around pore. 6. Collar cell, the nutritive cell of the endodermal layer.

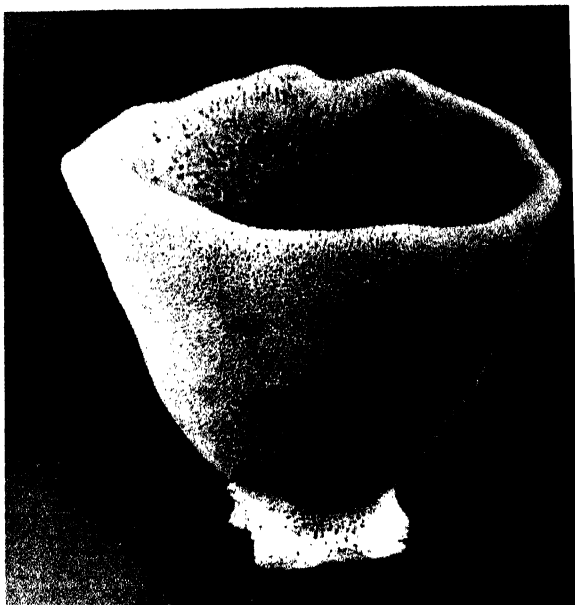
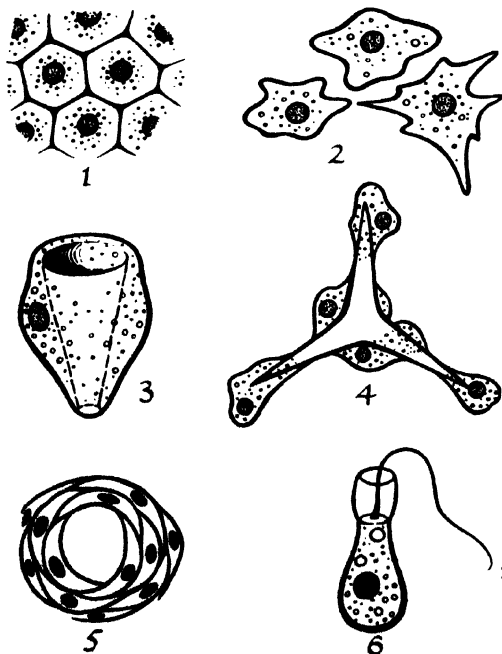


Fig. 234. A horny sponge — the elephant's ear sponge, with a pliable skeleton of spongin.

pockets within the pockets, so that the inner area is still larger and there is an intricate system of canals leading to pockets lined with collar cells. Obviously a sponge of this type can grow much larger than a simple bag sponge can, for while the body wall is thicker, the distance from the food-catching collar cells to the other cells has not been materially increased and yet the relative surface covered by collar cells has been vastly augmented.

The Living Sponge

A glance at the way a sponge actually lives will illustrate the simplicity of its design. It secures food by waving the flagella of its collar cells, thus setting up currents of water which draw in suspended food particles with them. The food particles are ingested by the collar cells and by the amoeboid cells in the mesoglea in typical amoeba style. Nutritive substances then diffuse to the other cells throughout the body, and wastes are eliminated by the same means. The adult sponge is not capable of movement, and the organism as a whole shows neither coordination nor perception, though the individual cells display these qualities in the ways all cells do. Thus a stimulus at any

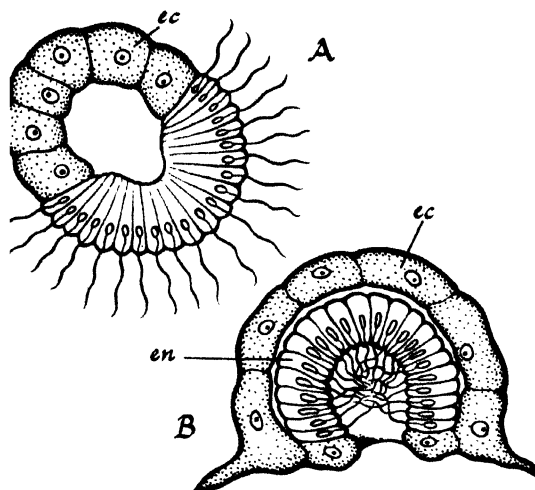


Fig. 235. Sections through larvae of a sponge. A. Ciliated larva. B. Infolding of flagellated cells to produce inner layer; outer layer is of non-flagellated cells.

one point affects only that point, except as it is transmitted from one reacting cell to another. The paramoecium is actually far more highly coordinated, though but a single cell, than is the multicellular sponge. Reproduction in sponges may be asexual, by simple budding, or by the separation of one part of the sponge from the main body. This may be accidental or a result of human action, as in the deliberate cutting done in the culturing of sponges. For commercial use, certain types of sponges are cultured by planting fragments of a larger sponge attached to stone weights in suitable spots on the ocean bottom. In several years

these grow sufficiently to be harvested. The living tissue is then subjected to a rotting process, the horny skeleton is washed clean, and the commercial sponge is ready for use. Today many synthetic sponges are made of rubber or other plastics.

Many sponges reproduce asexually by enclosing numerous mesogleal cells in a durable protective covering studded with siliceous spicules. This entire object, called a *gemmule*, eventually bursts, releasing amoeboid cells, which then cooperate to form a new sponge. Reproduction may also be sexual through the formation of gametes. The eggs, fertilized within the body of the parent, develop into ciliated larvae (Fig. 235) which swim about, settle down on a solid object, and then by an infolding process develop into a mature sponge.

Protozoan Relationships

Sponges show striking relationships to their presumed protozoan ancestors. Among these are the flagellated collar cells, the amoeboid mesogleal cells which ingest food into food vacuoles like a rhizopod, the ciliated larva with its flagellum-bearing cells, the general lack of systematic organization, and the relative independence of the cells indicated by the absence of any coordinating system. An experiment may be cited that emphasizes this last point especially well. If a sponge is pressed through a piece of bolting silk, so as to separate its constituent cells from each other, these cells will reassemble by amoeboid action into a new sponge (Fig. 236).

Yet in spite of such primitive characteristics

Fig. 236. Separated sponge cells (left) reassembling (at right).



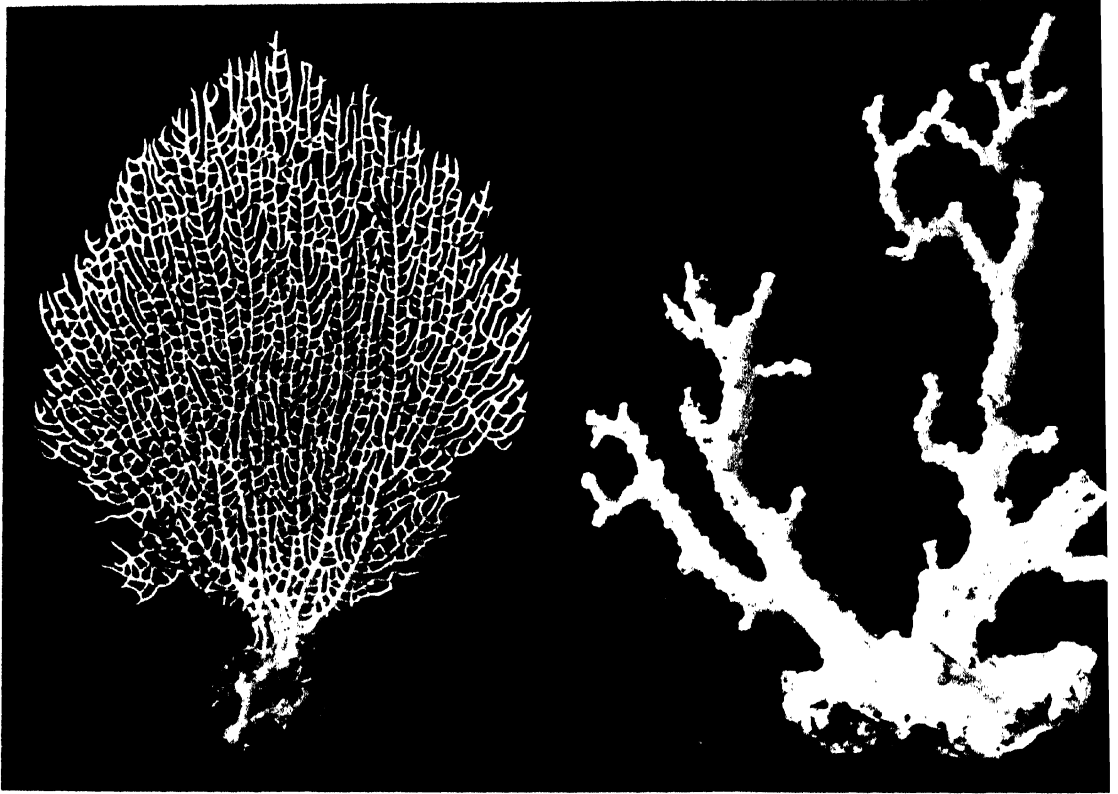


Fig. 237. Types of coral. *Corallium elatior* from Japan. *Rhipidogorgia flabellum*, from the Bahamas.

as their clear protozoan relationships, their sessile mode of life, and their lack of coordination, the sponges show notable advances over simple colonial organisms, especially in having a central cavity provided with openings and in having the beginnings of separate tissue layers. While they are a divergent line not ancestral to higher animals, they show the first steps in metazoan organization.

METAZOA WITH TRUE TISSUES: THE COELENTERATES

Diversity and Distribution

Stemming from a different group of protozoan ancestors is another group of simple metazoans, the phylum *Coelenterata* (Gr. *koilos* = hollow + *enteron* = intestine). These are a successful and diverse assembly of animals, living in a world as strange and almost as different from ours as any we might dream of, though we may have been within a dozen feet

of it without guessing its presence (Figs. 237-238). Its margins lie along the shores of our great oceans, and anyone may enter it with a simple bucket helmet, a length of hose, and a hand pump. As little as twenty feet below the surface lies this soundless world, bathed in a restless green translucence. Here are strange bushes and grasses, great colonies of minute coral polyps, coelenterate builders of coral reefs. Some of these pastel blossoms reach out and grasp jeweled fishes and slowly draw them into hidden mouths within their crowns of tentacles. These are the sea anemones, carnivorous coelenterates despite their flower-like appearance. Gossamer shapes, unmatched in the world of air and sunshine, drift by in clouds of thousands, like swarms of soap bubbles. These are the jellyfishes, also coelenterates, many of them shaped like inverted crystal bowls, shimmering blue and pink, and trailing films of lace, yet threatening death to many a small fish or crustacean.



Fig. 238. Sea anemones, "flowers" of the marine world, occur in many pastel colors. Many forms possess nettle-bearing threads that may be hurled out through the mouth or through body pores. Anemones can move by gliding movements of the disk-like foot.

The coelenterates are as varied in habitat as in form. Some live in tropical seas, some in the Arctic, and some are world-wide in distribution. They range from tidal zones to the icy blackness of three-mile depths, and a few, like the hydra, have invaded fresh water rivers and lakes. Some are sessile, like the sea anemones, and the corals. Others alternate between sessile polyps and free-swimming medusae or jellyfish forms. Still others, like the largest jellyfishes, spend their entire lives floating freely in the ocean. Coelenterates may live singly, like these, or they may live in vast colonies of thousands, like the coral polyps, which merge with similar colonies to produce complexes of millions. These pile generation upon generation of limestone skeletons, thus building great coral reefs a thousand or more miles in length. Where coastlines sink, the endless building of coral polyps may continue to raise the reef their ancestors have constructed, thus forming the picturesque fringes around tropical islands; or, where islands have submerged, forming circular atolls harboring sheltered lagoons. These mightiest of coelenterate structures, or indeed of any structures built by living things save man, are the products of some of the smallest individuals of their phylum. Other coelenter-

ates, like the sea anemones, may grow to a diameter of three feet, and may attain an individual age of seventy years or more. As a group, the coelenterates are ancient, for jellyfishes have left their imprints in Cambrian rocks a half billion years ago, while corals appeared in the following period, the Ordovician.

Symmetry

Since the coelenterates are all either sessile or drifters in open water, they receive stimuli from every side. But because most stimuli affect the mouth end, increased responsiveness in that region has had selective value and accounts for a concentration of nerve cells in that region. Thus the coelenterates have taken a first step away from the most primitive body organization, or symmetry, in the direction of that found in the higher animals and in man. They have developed a head end.

Three main steps may be defined in the evolution of symmetry (Fig. 239). Many of the simpler creatures, such as the colonial *Volvox*, are symmetrical with respect to a central point, like a sphere. Any plane which passes through this point divides the animal into symmetrical halves, and any such "half" is exactly like any other. The coelenterates are a distinct step beyond this. They have a head or anterior end crowned with tentacles and a base or posterior end, in sessile forms equipped with a foot. They are not, however, divided into "sides," but like a cylinder are symmetrical with respect to a single axis running lengthwise through the body, so that any side is like any other. The third stage in symmetry, the bilateral, does not appear until the emergence of more complex organisms, and is first seen in the phylum Ctenophora, which will be briefly considered at the end of this chapter. Animals which are bilaterally symmetrical not only have anterior and posterior ends, but also a belly or ventral side and a back or dorsal side, so that they are symmetrical with respect to a single plane only, which divides them into right and left halves.

With these changes in symmetry comes increased coordination, which in turn brings greater directional mobility. To pursue food

appears to be more successful than passively to wait for it, and as radial symmetry gives greater power in this than spherical, so bilateral symmetry gives more than radial. As radial symmetry seems to have come about through the development of a differentiated mouth end, bilateral symmetry probably appeared with the specialization of belly and back sides. Thus if a hydra, a simple coelenterate, were to acquire more freedom of movement, it might move with its mouth end foremost. In doing so, that side of its body nearest the bottom of the pond would be exposed to different stimuli than the upper side. In time, selection would lead to organisms with adaptive differentiation between the belly or ventral side and the back or dorsal side. This would mean the beginning of bilateral symmetry. While this development does not appear among the coelenterates, these creatures nevertheless seem to be on the main line of evolution toward the higher animals.

The Coelenterate Pattern

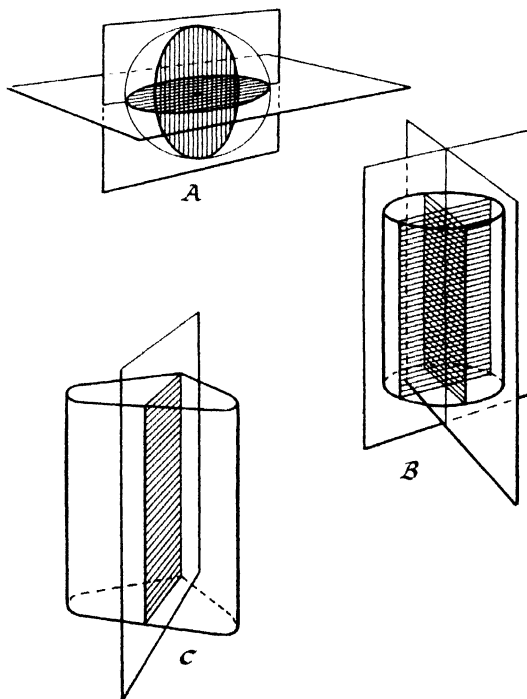
In the coelenterate body, which is more definitely organized than that of the sponges, the basic metazoan pattern begins to emerge. There is a central body cavity, called the gastro-vascular cavity since it serves for both digestion and distribution. At one end of this is a mouth, through which food is taken in and wastes are egested. This opening is surrounded by tentacles, which capture the animal's prey and draw it to its fate. Around the body cavity all the cells are neatly arranged in two principal layers, the ectoderm or outer covering and the endoderm or inner layer, which lines the gastro-vascular cavity. Between these is a non-cellular, jelly-like mesoglea. In the coelenterates there are many more kinds of specialized cells than there are in the sponges. There are, in particular, always complex and unique stinging cells. But even more striking is the sharper division between the functions of the cell layers and, as a consequence, the increase in efficiency.

There are two basic body forms among the coelenterates. One is the *polyp* (Gr. *polys* = many + *pous* = foot) and the other is the

medusa or jellyfish. The polyp body is a tube, closed at one end, and crowned at the other with a ring of tentacles around the mouth. The medusa is a structural modification of this form. Imagine a polyp compressed along its longitudinal axis, with its mesoglea enlarged to a jelly-like mass, and then the whole structure turned upside down — that is the pattern of the jellyfish (Fig. 240).

There are many modifications of these two simple plans. The *Hydrozoa* (Gr. *hydra* = a serpent + *zoon* = animal) are small individual polyps with a simple, undivided gastro-vascular cavity. Some, like the hydra, live independent, individual lives, while others form colonies of considerable size. In many there is an alternation of generations between polyp and medusa phases, though the former is chief. The polyp-like *Anthozoa* (Gr. *anthos* = flower), though built on the same pattern, are larger and more elaborate, since in them the gastro-vascular cavity is partitioned. They do not have an alternation of generations. They range in size from microscopic corals to three-foot sea anemones. A third group, the class *Scyphozoa* (Gr.

Fig. 239. Three plans of symmetry found in organisms: A. Spherical; B. Radial; C. Bilateral.



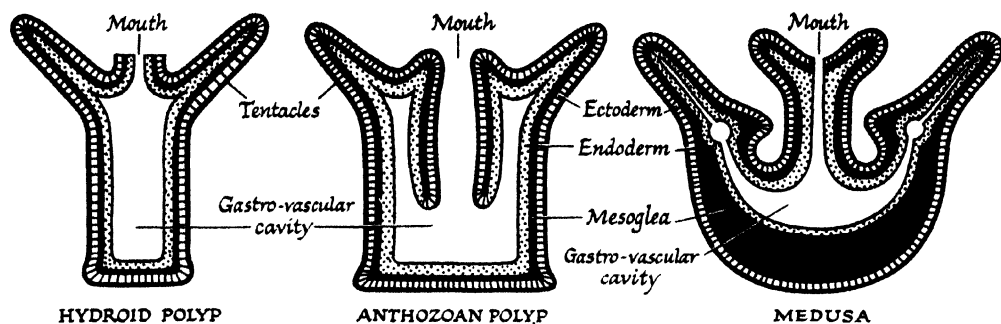


Fig. 240. Coelenterate body plans. The medusa is here shown mouth up for comparison, though normally it swims mouth side down.

scyphos = cup), is mainly of the medusa type. Some scyphozoans produce polyps, but these are small and relatively degenerate, and the medusa is the principal phase. Jellyfishes cover a wide range in size. Some of the giants of the open ocean reach a diameter of seven and a half feet and have a tentacle spread of a hundred feet.

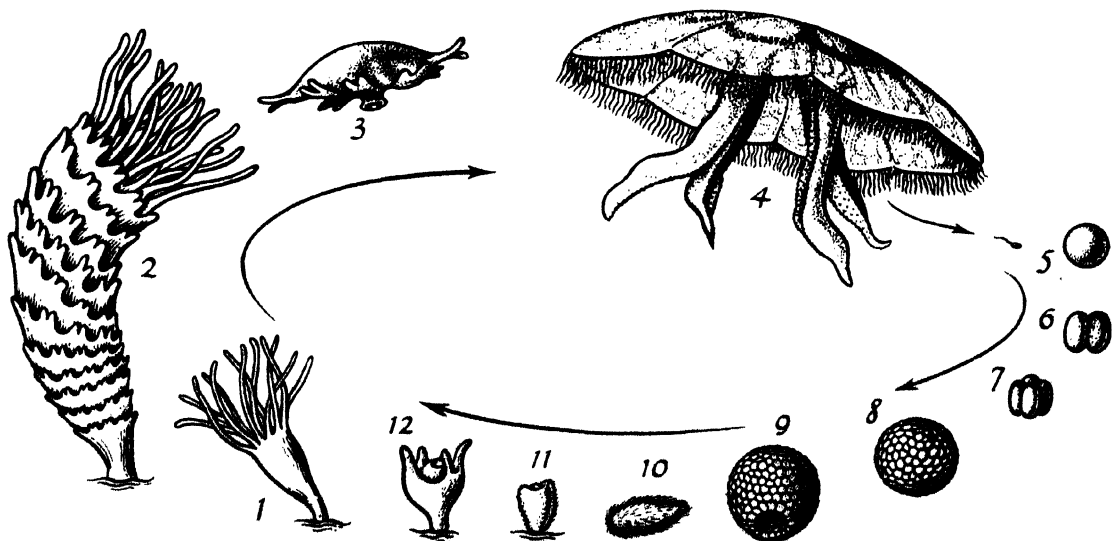
Alternation of Generations and Polymorphism

The immense variety found in the coelenterate way of life is emphasized by the fact, already noted, that in many species there is an alternation between polyp and medusa forms from one generation to the next. Moreover, the

polyps themselves are frequently polymorphous, that is, of different forms, and show at least a differentiation between feeding and reproductive types. The latter produce rows of buds which eventually break off and swim away as small jellyfishes. The latter are the sexual generation and reproduce by eggs and sperms discharged into the water. The zygote develops into a small ciliated larva (a planula) which, after attaching itself to any convenient solid object, becomes a polyp, and thus the cycle is completed.

In some coelenterates, like the hydra and the sea anemones, there is no medusoid phase. Among the scyphozoans, to which belong the

Fig. 241. Life cycle of *Aurelia*. 1. Young hydroid polyp phase. 2. Same with many terminal buds. 3. One saucer-like bud detached. 4. The mature jellyfish, with gonads which produce eggs and sperm. 5. Eggs and sperm, greatly magnified. 6. First cleavage produces a two-cell stage. 7. A second cleavage produces a four-cell stage. 8. The hollow blastula. 9. Gastrula, formed by invagination. 10. The ciliated planula larva. 11. The planula attaches itself to a solid base. 12. Planula becomes a polyp.



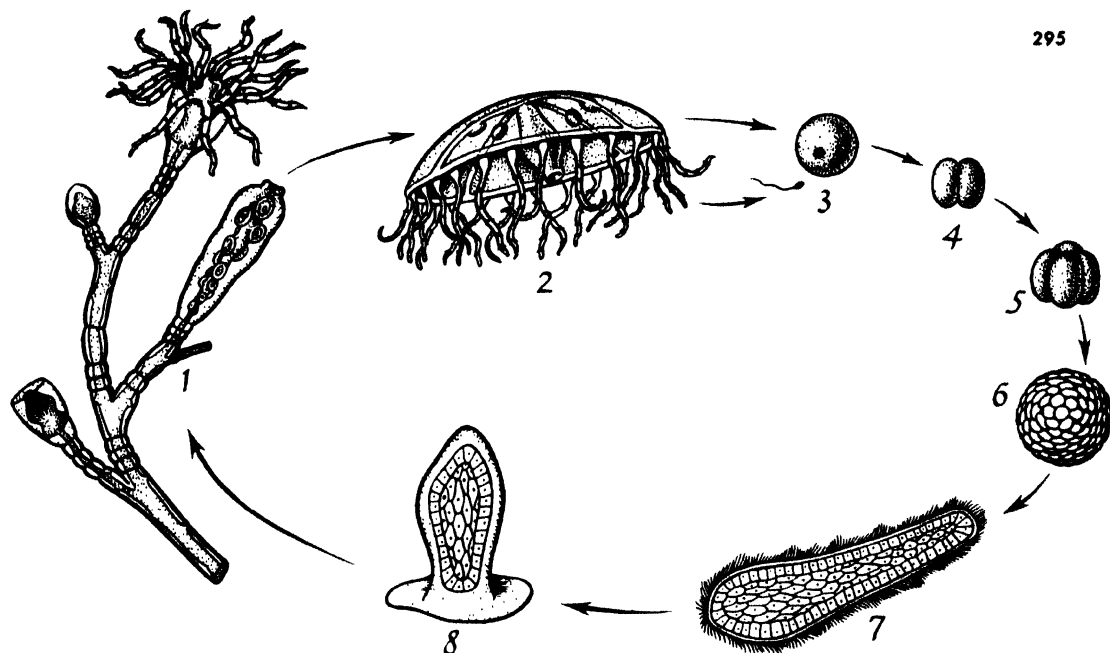


Fig. 242. Life cycle of *Obelia*, a colonial hydroid. 1. Portion of colony with feeding and reproducing polyps. The latter asexually produces the medusae. 2. The sexual phase, the medusa. Lumps on radial canals are gonads. 3. Egg and sperm. 4, 5. Stages of cleavage. 6. The blastula. 7. The ciliated planula larva. 8. The planula attached and becoming a polyp.

giant jellyfishes, the hydroid phase may be reduced or entirely suppressed. *Aurelia*, one of these, spends most of its life as a medusa (Fig. 241). It reproduces sexually, and the zygote develops into a ciliated larva, which gives rise to a polyp. Degenerate and much reduced, this polyp repeatedly sections itself horizontally by forming a series of terminal buds, like a stack of saucers. One by one these break off and float away as miniature jellyfishes, and each then grows into a new *Aurelia* medusa. Here the polyp phase has degenerated into nothing more than a structure for rapid asexual reproduction.

Between these extremes is almost every imaginable variant. *Obelia*, a colonial hydrozoan (Fig. 242), is a typical coelenterate with two well-balanced reproductive phases. Its planula larva produces a polyp which, in turn, produces a whole colony of attached polyps by subsequent budding. These are of two kinds, feeding and reproductive. A rigid secretion of the ectoderm forms a cup around the base of each feeding polyp, which may withdraw into it for protection. Around the reproductive polyp,

this secretion forms a closed, club-shaped case, within which, upon the stalk-shaped body of the polyp, medusa buds form. These eventually become free-swimming jellyfishes. On these, gonads develop along the radial canals of the digestive tract leading from the mouth to the margin of the bell-shaped creature. Eggs and sperms are discharged into the water. Cleavage produces the planula again, and the cycle is complete.

In some coelenterates, such as the Portuguese man-of-war (Fig. 243), polymorphism reaches astonishing extremes. In this colonial creature some polyps unite to form a gas bag, or float, while others feed the colony, and still others only receive stimuli. Some of the polyps sting and others bud off egg-producing medusae. None of these polyps is capable of an independent life, and the whole colony has been fused into a super-individual almost as united and interdependent as the cells in the human body. Here a third level of organization has been reached. After the cell and the metazoan individual comes now the polymorph metazoan super-individual: a new order of being.

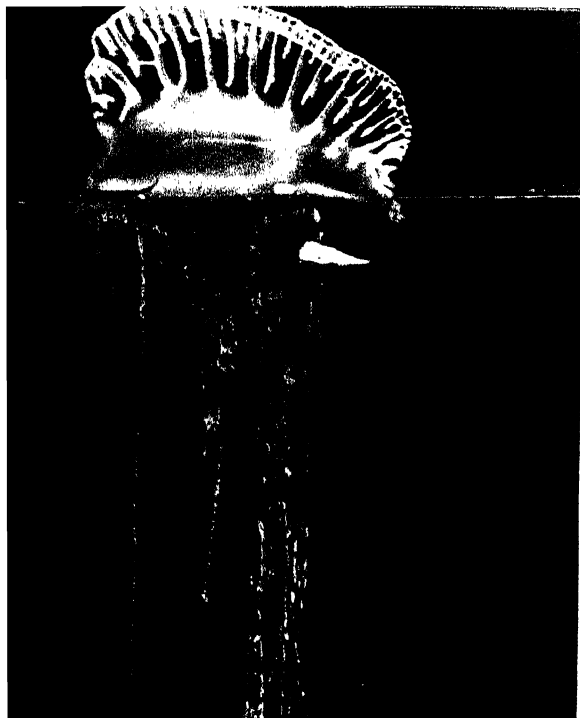


Fig. 243. *Physalia*, the Portuguese man-of-war. This one has captured a fish by paralyzing it with stinging polyps. Shimmering in colors of mother-of-pearl, these polymorph hydrozoan colonies are lovely to look at but deadly to approach.

HYDRA: A SIMPLE COELENTERATE

The basic features of the coelenterate body (Fig. 240A) can be seen in the *Hydra*, though its simplicity is not fully representative of the diverse marine coelenterates which make up the bulk of this great phylum. Hydras may be found in almost any body of clear cool fresh water.

Although a fully relaxed hydra may reach a length of almost two inches, it is still virtually microscopic, for in this extended condition it is thinner than a hair. Contracted, the same hydra will be no larger than a small pin-head (Fig. 245). By its disk-like foot it can attach itself to the leaves or stalks of aquatic plants, frequently hanging head down, with its tentacles forming a fine thread-like curtain. Frequently small water animals, blindly bumbling through the water, swim full tilt into the tentacles. The hydra quickly responds by a spasmodic contraction of its body and tentacles. At the same time microscopic poisoned

darts shot out from the tentacles penetrate and paralyze the victim. The tentacles then slowly drag it to the edge of the purse-like mouth, which creeps over the prey, much as a rubber bag might be drawn over a larger object, until eventually the victim is completely engulfed. In this manner a hydra can ingest an animal several times its own size. The hydra moves by a crawling action of its foot, or by turning repeated somersaults.

Cell Specialization

Although the hydra is considerably larger than most protozoans, its individual cells are much smaller but surprisingly diversified. The body wall contains about eight different kinds of cells in addition to its gametes (Fig. 244). Most of the outer covering is formed of block-like cells, each with a protoplasmic strand at its base capable of marked contraction. This strand serves as a muscle, and the cells are called epithelio-muscle-cells. Between these, sometimes singly, sometimes in large clusters (especially in the tentacles), are the stinging bodies or *nematocysts*. These are highly specialized devices formed inside special cells. The nematocysts are deadly structures and small miracles of efficiency. Each consists of a bulb within which there is coiled a hollow thread, actually a projection of the bulb inverted into itself. At the base of the thread are several sharp spines which emerge point foremost when the nematocyst explodes, tearing holes into any reasonable obstruction they meet. A paralyzing toxin is discharged through the tubular thread. In the hydra there are four different varieties of nematocysts — an interesting evidence of the degree of cell specialization found in this simple metazoan. Hundreds of nematocysts may strike a small aquatic animal at once. Each bulb is a one-shot weapon, and new ones are made from undifferentiated cells lodged between the more specialized ones. The immature cells which produce nematocysts, by amoeboid movement, migrate as needed.

Projecting to the outer surface between the epithelio-muscle cells are slender sensory cells, which react to external stimuli. These estab-

lish contact with an intricate network of co-ordinating cells located mainly in the mesoglea. In none of the simpler multicellular organisms so far discussed is there any such system of cells exclusively devoted to coordination, though systems of fibrils no less intricate than this are to be found in the more highly evolved protozoa.

In the endoderm of the hydra there are no less than four different kinds of cells. There are digestive cells, some of them flagellated and some forming pseudopods and food vacuoles, the latter also having contractile fibers in their basal region to assist in body movement. Whereas the fibers in the epithelio-muscle cells run lengthwise, those in the endodermal cells run circularly around the animal. Thus when the ectodermal fibers contract, the body shortens, but when the endodermal ones contract, it is squeezed out thin and long. Contraction withdraws the hydra from danger, and the fibers of the ectodermal cells are appropriately the more powerful.

A second kind of cell in the endoderm does not ingest food particles but aids in food preparation by secreting digestive enzymes. These are gland cells, whose action breaks up food in the gastro-vascular cavity into small particles that can be taken in by the digestive cells. Specialized sensory cells, similar to those in the ectoderm, are wedged between the others.

The "Tissue Level" of Organization

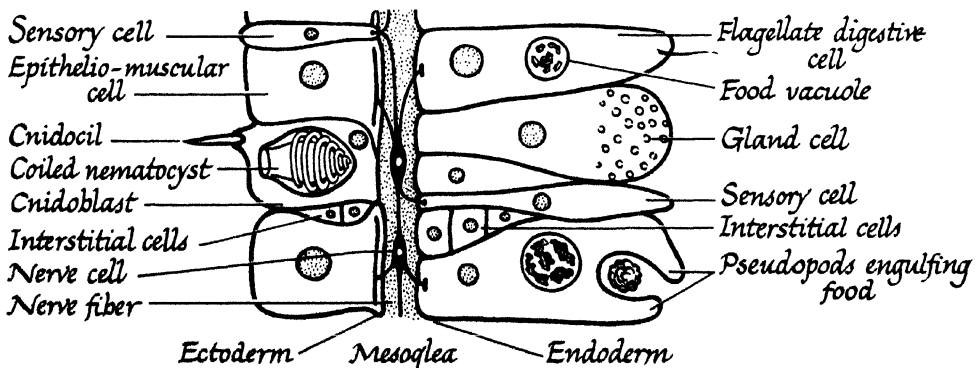
The most striking difference between the hydra and higher organisms, such as man, lies not so much in the structures it has as in those it still lacks. Like the higher plants, a hydra is built on what may be called the tissue level



Fig. 245. A hydra with a bud. This is *Hydra littoralis*, found in running water. The specimen shown is extended to its full length. Magnification about 6 X.

of organization. There is barely an indication of that knitting together of special tissues with complementary functions into the sorts of complicated organs, such as heart, liver, kidney, or stomach, which are characteristic of higher animals. Thus while more complex than the sponges, the hydra must still carry on its animal functions in a very simple way indeed.

Fig. 244. Longitudinal section of the body wall of *Hydra*, showing position of different kinds of specialized cell.



Dissolved food substances are distributed through the gastro-vascular cavity — which thus serves both as a digestive organ and a distributing system, and which extends throughout the body (Fig. 240A) to the tips of the tentacles. Since the body tissue is never more than two cells thick, no cell is more than one cell distant from the source of food. Wastes are egested simply by emptying the bag-like body through the opening that serves for filling it — not an efficient system, perhaps, but one which has worked well enough for the animal to have passed the screening of natural selection.

One notable development in the hydra is in its systems of coordination and perception, which are essentially like those of the higher animals though lacking in many of their refinements. While in the sponges a reaction is limited to the part of the body stimulated, in the hydra a stimulus applied at any point is carried by the network of nerve cells indiscriminately to all parts of the animal's body, and may result in a local or a diffuse general reaction depending on the strength and nature of the stimulus. Except for the concentration of nerve cells around the mouth of the hydra, there is no nerve "center," and no structure that may be compared to a nerve cord or a brain. For this reason consciousness or sensation as we understand these things cannot exist in the hydra. Its reaction to a stimulus is no more conscious than the twitching of a severed frog's leg. Nonetheless, the responses of the hydra are effective in helping it to obtain food and to avoid damaging influences.

Usually the hydra reproduces asexually by budding (Fig. 245). A portion of the body wall bulges, grows tentacles, develops a mouth, and eventually pinches itself off from the parent animal. In other coelenterates the severing constriction fails to occur, and thus colonies of hydroids come into being. Hydra also possesses remarkable powers of regeneration, which is not surprising when we consider that any segment of a hydra is almost exactly like any other. Even if cut into many segments, each bit will regenerate the missing portions.

In sexual reproduction, cells of the ectoderm produce eggs and sperms, either at the same time or alternately. The sperm cells are produced in great numbers and are discharged into the water. The egg cell increases greatly in size by absorbing nourishment from other cells around it, and, when mature, is fertilized by a swimming sperm. The fertilized egg develops into an embryo before it is released from the parent. A protective coating having been secreted over it, it falls to the bottom of the pond. Highly resistant to unfavorable conditions, it can live through periods of drought and low temperatures that would kill mature animals. Cross-fertilization is general. Again — Hydra is most notable for the organs it lacks.



The Coelenterates and Metazoan Evolution

Unlike the sponges, which appear to be on a divergent, dead-end evolutionary path, the coelenterates seem to represent the first important metazoan development, which in turn gave rise to higher animal forms. For this reason the evolutionary advances they exhibit are of considerable importance. Thus while sponges show some cell differentiation, in the coelenterates diversification has gone a good deal further. Not only is there a well-developed ectoderm and endoderm, but there is considerable specialization among the various types of cells. The diploblastic or two-layered arrangement of tissues appears to be a necessary forerunner of the triploblastic or three-layer system of the higher metazoans. In the hydra there is only a thin basement membrane between the two layers of cells, but in other coelenterates there is considerable mesoglea containing some cells, which foreshadow the third or central layer of the higher animals. Another important development is the appearance of the digestive cavity, around which the bodies of all higher metazoans are built. Extracellular digestion, which enables large objects to be eaten and digested, has replaced intracellular digestion, which must be restricted to minute particles.

The coelenterates show three other new developments: cells for coordination, forerunners of the nervous system found in higher animals;

the faint beginnings of cephalization or head-formation; and a first step toward the formation of real organs. The system of coordination enables the coelenterate to function as a unified organism rather than as so many individual cells, as in sponges. And the crowding of nerve cells around the mouth is probably responsible for the fact that in the higher animals and in man the brain is in the head end near the mouth. Lastly, the mouth, the tentacles, and the foot are body parts with special functions and may be thought of as rudimentary organs; and the two opposed sets of muscle fibers presage the system of motion and locomotion which, with the skeleton, makes possible the fleetest creatures of today.

THE CTENOPHORES: A TRANSITIONAL GROUP

Like some of the coelenterates, though more complex, are the members of a small phylum, the *Ctenophora* (Gr. *ktenos* = comb). Popularly known as sea walnuts and sea gooseberries, the more typical ctenophores have the same watery transparency as the jellyfish and, outwardly, the same radial symmetry (Fig. 246). But structurally they are a good deal more complex. They show a beginning of bilateral symmetry, and some of the less typical forms show startling resemblances to the flatworms, which we shall see in the next chapter. These things suggest that the group is transitional, and it is interesting to us mainly for this.

The ctenophores get their name from comb-like fused cilia arranged in eight meridian rows from the mouth on the ventral or lower end, to the opposite pole of their egg-shaped bodies. Two tentacles, one on either side of the body, express their bilateral symmetry, a significant change from the radial symmetry of the coelenterates. The mouth leads into a tubular gastro-vascular cavity which, unlike that of the coelenterates, is more or less branched. Moreover, the digestive tract opens at its upper end in two minute pores, which however do not function in egestion. By day the typical ctenophore looks much like a ball of jelly shimmering with opalescent colors, and at night it is brilliantly luminescent.

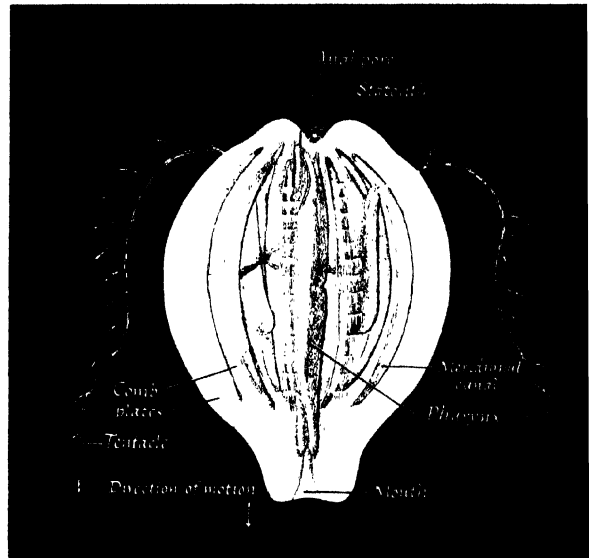


Fig. 246. *Hormiphora*, a typical ctenophore.

Perhaps of greater interest than the common ctenophores are some of the atypical ones. Venus' girdle (*Cestus*) is so pulled out into two flattened and greatly elongated lateral processes that it is much wider than long. Well-developed muscle fibers in a definite tissue layer lying between ectoderm and endoderm, the *mesoderm*, control its wave-like undulating motions. The development of mesoderm is a vast step beyond the typical coelenterates, except possibly the sea anemones.

Perhaps of greatest interest, because they suggest a transition between coelenterates and the next higher phylum, the Platyhelminthes, are the aberrant bottom-living ctenophores such as *Ctenoplana* and *Coeloplana*. Imagine a pliable ovoid ctenophore placed on the ground, mouth downward, and then flattened out as though stepped on, and the result is *Coeloplana*. Almost indistinguishable from some of the flatworms, both in appearance and in anatomy, the creature glides along the bottom or over the surfaces of marine plants. One ctenophore from a fiord in western Greenland (*Tjalfiella tristoma*) has even become sessile, and has, like a flatworm, a branched gastro-vascular cavity. Thus the comb-jellies indicate how bilateral worm-like creatures, such as the flatworms, may have evolved from the simple, radially symmetrical coelenterates.

The Metazoans Diversify

Greater complexity, more specialized adaptability, and almost explosive diversity — this is what we see as we go up the scale. Progress involves better coordination, with speedier action and more precision; increasing differentiation for locomotion, resulting in special organs such as tails, siphons, fins, and legs; increasing ability to receive the various stimuli of light, contact, heat, and so on; improved responses to stimuli through better organs of locomotion and through teeth, stings, and other structures; increased size and hence better protection; greater aggressive power and general ability to dominate the environment; physical structures which overcome the difficulties brought about by greater size and the higher rate of metabolism that goes with increased action, such as organs of respiration, excretion, digestion, and distribution; and methods of reproduction which eliminate some of the hazards to the young. All of these appear in the seven phyla with which this chapter will deal, those of the flatworms, the roundworms and wheel animalcules, the lampshells, the moss animals, the segmented worms, and the mollusks.

Perhaps as a result of their very diversity, we shall not find among the animals, as we did among plants, a single phylum in which the transition is made from water to land. Animals from many different phyla, varying considerably in the degree to which they have evolved, are found to have taken one or more steps toward life on land; and no one animal phylum can be given entire credit for this transition. There are no land sponges or land coelenterates, but aside from these almost every metazoan phylum has some forms which show adaptation to land life, even if most of its members are still wholly aquatic.

THE FLATWORMS

"Worms"¹ are of many kinds, yet even the simplest of them, the phylum *Platyhelminthes* (Gr. *platys* = flat + *helminthos* = worm) or flatworms, are as far beyond coelenterates and ctenophores in complexity as those are beyond sponges. These are the first animals with a true, fully developed *mesoderm* (Gr. *mesos* = middle + *derma* = skin) or third tissue layer in place of the simpler and often non-cellular mesoglea. From this central layer arise various internal structures, such as muscles and reproductive organs, which make for a great increase in efficiency. Moreover, the increased size made possible by such a three-layered body has been effective in bringing about other changes, including better coordination through centralization of nerve cells, better distribution of food substances, and an improved excretory system. The flatworms also have true bilateral symmetry and the increased specialization which often comes with it. In larval develop-

¹ Here a note on the word "worm." In early biology, most creeping things were called *vermin* (L. *vermis* = worm). Most moderns are more discriminating — though the term *vermin* is still widely used — outward body shape being no criterion of real relationship. In biology it is quite useless to speak of "worms," for the term refers to no definite organism or group. Organisms once so classed have been segregated into many phyla, though the idea of "worm" is retained in the Greek derivative *helminthes* (*helmins* + *inthos* = worm, especially an intestinal worm), as in the phyla *Platyhelminthes* and *Nemathelminthes*, flatworms and roundworms, respectively. Even here, "worm" has little significance. Many flatworms look less like worms than like slugs or snails, while certain worm-like marine creatures, such as the "acorn-tongue-worm" *Balanoglossus*, are structurally unrelated to any of the helminths.

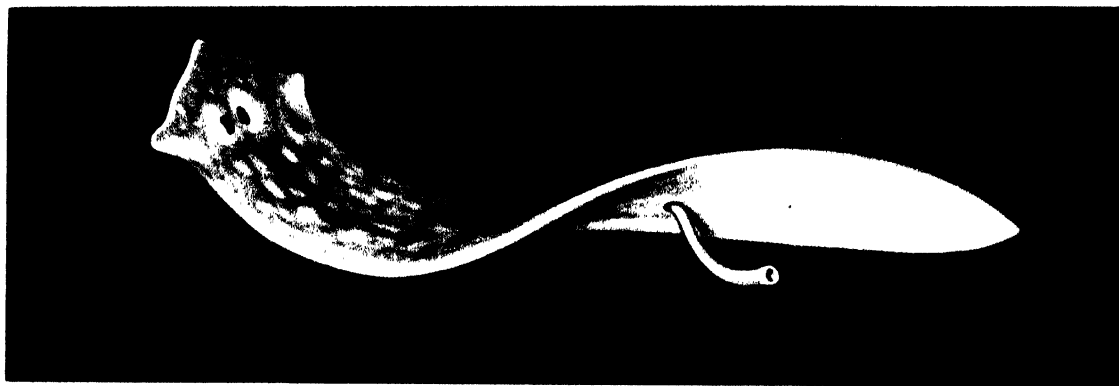


Fig. 247. *Planaria*, a common flatworm of the class Turbellaria.

ment, however, they suggest possible affiliations with the coelenterates and ctenophores, for the larvae of some bear cilia that are reminiscent of the comb-like cilia of the latter group.

The flatworms are a varied group, ranging from free-living, soft-bodied creatures found in fresh or salt water and even on land, to such parasites as the flukes and the long, segmented tapeworms.

Planaria: A Common Flatworm

One of the commonest and best known of the flatworms is *Planaria*, a member of the class *Turbellaria* (*L. turba* = disturbance, so called because the lower portions of their bodies are covered with cilia which disturb the water around them). Turn over a small rock in the bed of a clear stream or a stone in a hillside spring, and you may find one or more flat brownish creatures about a half inch long clinging to the bottom side. These are planarians, or common flatworms. On the head end is a pair of eyes that look perpetually crossed and two ear-like projections, the auricles. Although a planarian usually glides along the bottom by means of thousands of cilia that cover its under surface, it may even move out onto the underside of the water-surface, ventral side up. A slimy secretion makes a path along which the beating cilia propel the flatworm. If we turn a planarian on its back, it at once twists its body in a spiral, head end first, and soon is once more right side up. After gliding about for some time, it is likely to come to rest in the darkest spot available, and to assume the shape of a formless lump.

If we drop a small piece of liver into the water, we may see the planarian feed. Instead of going at its food head first, it glides over it and everts a whitish, trunk-like tube from the middle of its under side. This is a muscular syphon, the pharynx, which sucks in juices and loose particles from the morsel and is usually carried withdrawn into a sheath beneath its body. We recall that certain bottom-living ctenophores also have a central mouth.

Under the microscope, the most striking structure visible in a depigmented planarian is its much branched and lobed gastro-vascular cavity, consisting of three main tubes, one branch extending from the pharynx into the head and two branches extending toward the rear end of the body and more or less parallel. There is only one opening into this system, by way of the pharynx. Thus it is basically like that of a coelenterate, except that it is tubular and branched (Fig. 248).

In place of the hydra's diffuse network of nerve cells, the planarian has a ladder-like structure with relatively concentrated nerve tissue in the head end. This is a real centralized nervous system, barely foreshadowed in the coelenterates. The excretory system of the planarian consists of a network of fine canals running the length of the body in two lateral systems. At the inner ends of these canals are *flame cells* (Fig. 248), each like a goblet containing a tuft of flickering cilia looking like a candle flame. The canals link with several excretory pores.

Surrounding the digestive cavity is a single layer of endodermal cells, some of which are

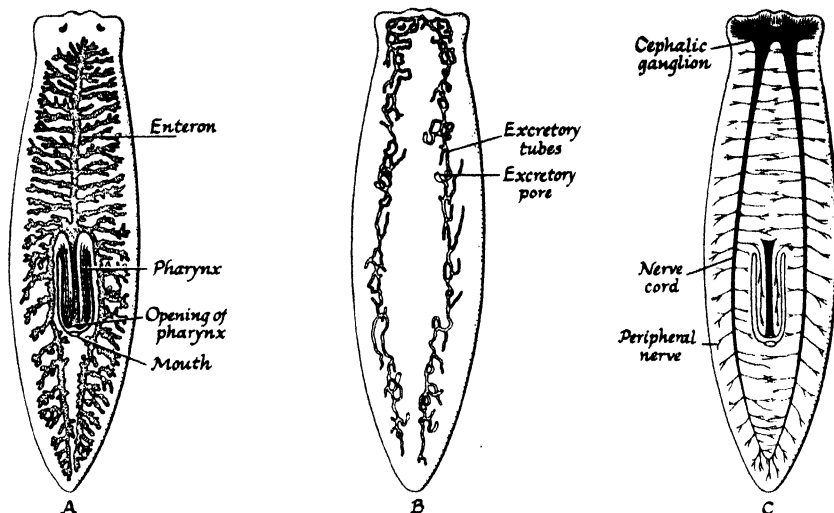


Fig. 248. Three organ systems of *Planaria* (diagrammatic). A. Digestive system. B. Excretory system. C. Nervous system. (After Wolcott.)

amoeboid ingesting cells and some glandular, much as in the hydra (Fig. 244). The outer coat of the animal is a single layer of ciliated ectodermal cells. Filling all the space between these two layers, the thick mesoderm consists largely of undifferentiated connective tissue cells separated by irregular spaces. Imbedded in these are highly differentiated muscle and gland cells and the complex excretory, nervous, and reproductive systems. The muscle cells are arranged in antagonistic sets as in the hydra, some fibers running transversely just beneath the ectoderm, while others deeper in the body run lengthwise. There are also diagonal fibers, which enable the animal to twist its body, and dorso-ventral fibers which make it flatter. Together with the cilia, these four groups of muscle fibers give the animal considerable control over its movements.

How Planaria Lives

Food taken in by the sucking pharynx is already in a partial state of dissolution, and there is little digestion in the gastro-vascular cavity. The food particles are taken up by the pseudopods of the endodermal cells and are largely digested within their food vacuoles. Digestion is still intracellular. Food substances then diffuse into the body fluids and so reach all other cells in the body. If the digestive sys-

tem of a planarian were local, as in many higher animals, this distribution would be wholly inadequate. But since the digestive tract branches so profusely into every corner of the organism, food readily reaches the most distant tissues. Distribution is, in fact, largely accomplished before digestion occurs, quite as in the coelenterates.

In so small an animal, each cell has sufficient access to the water in which the worm dwells to maintain adequate respiration, and no special respiratory system is to be found. Because of the greater activity of these creatures, their metabolism is generally higher than in the coelenterates. During prolonged starvation, a planarian can live on itself, consuming its own tissues in order to remain alive, and so in the end may shrink to less than one sixth its original size.

Compared to the diffuse and sluggish movements of the coelenterates, those of a planarian are precise and almost rapid. This is because the creature has four sets of muscle fibers instead of two, and also because it has a nervous system and even sense organs of a simple sort. In efficiency, the centralized nervous system of the planarian compares to the nerve net of hydra much as a modern city telephone system compares to an old-fashioned circuit system. In the latter, when one phone rings

they all ring, and everybody rushes to answer: a general alarm brings a general response. In the modern system, a central station directs the impulses over the right wires to just the phone for which the message is intended. This kind of selective coordination partly accounts for the refinement of motion in the planarian, as seen in its ability to turn itself right side up again.

The animal also has sharper contacts with the outside world. Beyond the usual senses of the epidermis, such as response to touch and temperature and perhaps chemical stimulus, it has eyes, and the whole body seems to respond to changes in light intensity, for destruction of the eyes does not completely destroy a planarian's response to light. Also the auricles, the small projections at either side of the head, may be organs of some special sense.

It is difficult to avoid anthropomorphism in dealing with the sense perceptions of animals. To call our senses five — sight, touch, taste, smell, and hearing — is a crude classification tied directly to the organs of perception we human beings happen to have. But perception is not limited to these senses, nor is it certain that the same stimuli affect other organisms as they affect us. The fact that a planarian or an earthworm responds to light is no proof it sees in the same way we do. Light in the long end of the spectrum so affects our eyes that we interpret the stimulus as red. The same stimulus to our skin is interpreted as heat. Saccharine tastes sweet to us, like sugar. But a fly easily distinguishes between the two, for it responds positively to sugar but negatively to saccharine. Thus to say that a planarian appears to "taste," apparently with its auricles, is to speak in anthropomorphic terms. If it seems strange that an animal responds to stimuli we cannot perceive, consider the many agents which produce no response on our organs of perception, such as radioactivity, ultraviolet light, and radio waves.

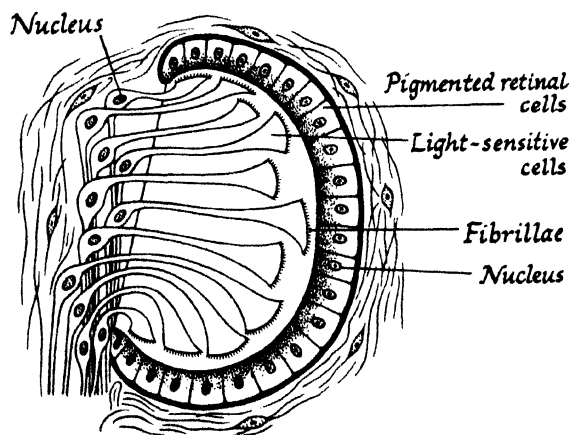
The eye of a planarian clearly perceives light, yet its ability to "see" is probably no better than that of a human being with his eyes closed. Nor does its response to light after its

eyes have been destroyed mean that it sees with its skin, any more than we see red light with our skins. The planarian also responds to vibrations in the water, but does it hear? We can perceive the vibrations of a radio through a sheet of cardboard held in the hand, but is that hearing?

In the eye of *Planaria* (Fig. 249), the pigmented cells form a cup or bowl which insulates the visual cells within it against all light except that which enters through the open side of the bowl. Light shining at an angle into the bowl will stimulate only those visual cells at the opposite side. Since the direction of the light determines which visual cells are stimulated, the planarian can determine which direction the light comes from. This is probably the full extent of its ability to "see." No kind of image is possible with such equipment. Similarly a planarian's sense of "taste" is probably extremely limited; and sound, as we know it, probably does not exist for the creature.

Planaria may reproduce asexually by transverse fission, with very little preparation or ceremony. The hind end and the front simply part company, and each grows the missing portions and becomes a complete new individual. Experiments have shown that growth-controlling gradients exist in *Planaria*, similar to those in the willow branch (page 229). Thus a portion containing a head will produce a tail. A tail end will produce a head. A middle piece

Fig. 249. Section through eye of *Planaria*.



will produce both. And a mid-section that would produce a head if attached to a tail produces a tail when attached to a head. When the head of a planarian is slit into several flaps, each flap can replace the parts from which it was separated, and thus monsters with multiple heads can easily be created. Yet this regenerative power, so amazing in the sponge, and still quite remarkable in the planarian, tends to diminish steadily as animals become more complex. Who needs to be told that a human being cannot even regenerate the tip of his little finger?

Sexual reproduction also occurs in *Planaria*. Well-differentiated eggs and sperm cells are both produced by the same individual. Planarians are thus hermaphroditic (Gr. *Hermaphroditos*, a son of Hermes and Aphrodite, who while bathing became joined in one body with a nymph), but the reproductive system is so constructed that the animal can no more fertilize its own egg cells than an earthworm (pages 321-322).

In some marine flatworms there is a larval form, the *protrochula*, which resembles both the larvae of nemertine worms (page 307), and the trochophore larvae of the annelids and mollusks (page 312). These trochophores, in turn, resemble the rotifer *Trochosphaera*, (Fig. 257), and thus suggest a phylogenetic relationship among all these groups.

Planaria, in short, shows remarkable advances over the coelenterates. Its bilateral symmetry goes hand in hand with cephalization, the development of a nervous system in the head end. The appearance of a mesoderm paves the way for the development of organs and organ systems and for more groups of muscle fibers essential for diversity in movement. And with the central nervous system come special sense organs, especially the cup-shaped eye, and sensitivity and response to the environment are increased.

Parasitic Flatworms: The Flukes

While the turbellarians, like *Planaria*, are all free-living, there are a great many parasitic flatworms, among them the *Trematoda* (Gr.

trematodos = having pores), commonly called flukes. These are unciliated animals with a firm cuticle or outer covering and frequently with many suckers or pores. Like most parasites, the flukes differ considerably from their free-living relatives, mainly in the degeneration of structures not functional in their mode of life and in the development of special structures adapted to parasitic living. While all organisms struggle to survive and reproduce, this struggle seems especially pronounced in parasites. Successful ones usually gain the advantage of almost unlimited and easily accessible food. But the difficulty of transferring their offspring to a new host largely nullifies this advantage. Hence the survival of a parasite usually hinges on its ability to produce enormous numbers of offspring. Indeed, the bodies of many are little more than sacs of reproductive structures, and most of the other functions of free-living animals are performed by the host. There are many degrees of parasitism among the trematodes. Some are only superficially modified, and live as external parasites attached to the outer surface of fishes, feeding upon their tissues. Others are highly specialized internal parasites, many with extremely complicated life cycles that involve several intermediate hosts.

The Liver Fluke of the Sheep

Fasciola hepatica, the liver fluke of the sheep, which is fairly representative of the group, is basically similar to *Planaria*, though it has lost its eyes, lacks cilia, has suckers for attachment, and has a highly developed reproductive system. The adult fluke lives in the liver and the bile duct of the sheep (Fig. 250), where it causes the disease known as "liver-rot," which may be fatal. The fluke itself looks like a small flat tongue about an inch long.

The life cycle of *Fasciola hepatica* is generally characteristic of the class. Fertilized eggs discharged into the bile duct of the host by the hermaphroditic adult fluke find their way into the intestine and are discharged with the feces. The egg must drop into a moist or swampy place if it is to survive. In the water, it de-

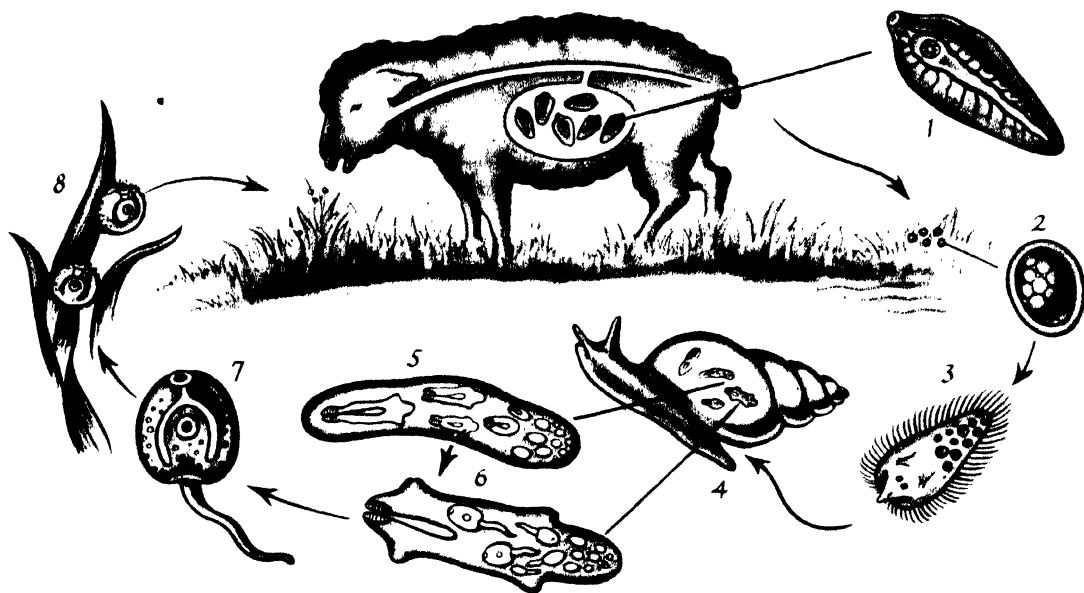


Fig. 259. Life history of the sheep liver fluke, *Fasciola hepatica*. The adult worms in the bile duct of the sheep lay eggs (2) which become ciliated larvae (3), which bore into the snail *Lymnaea* and there produce sporocysts (5) and rediae (6), two types of reproductive sac. Rediae in the liver of the snail may produce daughter rediae or cercariae (7), tailed swimming larvae that emerge from the snail, swim about, and encyst on grass (8).

velops into a small ciliated larva, which, significantly, has eyes. This bores into a snail of a particular species, and through a series of asexual reproductive phases increases enormously in numbers. First the larva becomes a *sporocyst*, a muscular sac. Without fertilization, each egg produced in the sporocyst develops into a second form of reproductive sac (a *redia*), which may now produce many more sacs of the same kind, or a number of tailed larvae (*cercariae*). These escape from the parent sac and then from the snail, swim about in the water and then encyst on a blade of grass. This cyst must be eaten by a sheep in order to complete the cycle. It is clear that the chances for any particular egg to mature are minute.

Despite so complex a life cycle, we cannot consider *Fasciola* a highly effective parasite, for while it is completely dependent on its host for its own survival, it is often fatal to its host. A parasite which causes the death of its host clearly tends to hasten its own extinction. Long-established parasites have usually evolved concurrently with the host, so that the survival of the host in the presence of the parasite is

possible. Thus organisms frequently tolerate indigenous parasites or diseases without marked damage, whereas foreign organisms frequently react violently to the same parasites.

Other trematodes have a far-reaching effect on millions of human beings. In China, Japan, Egypt, Africa, and South America, millions of people are infected yearly with various species of flukes. Where they do not kill outright, they cause great suffering, marked anemia, and general weakening of physical powers and of resistance to other diseases. In some areas, almost the entire population is infected, so that the backwardness of certain regions, particularly Egypt, is contributed to by the energy-sapping effect of trematodes. This scourge could be eliminated by simple measures of sanitation that would break the cycle of infection, such as disposal or treatment of human excrement, care in the choice and sterilization of the water supply, and exclusion of raw fish from the diet, for the larvae of many flukes encyst in fishes.

Parasitic Flatworms: The Tapeworms

Even more highly specialized as parasites are the tapeworms, of the class *Cestoda* (Gr.

kestos = girdle). Although they infest the intestines of many animals, both domestic and wild, as well as that of man, the damage they cause is generally not severe.

Tapeworms are usually long, ribbon-shaped organisms consisting of many similar sections, or *proglottids*, which are little more than sacs containing reproductive structures (Figs. 251 and 252). There may be only a few proglottids or many hundreds, depending on the species — and some tapeworms reach the astounding length of eighty feet. Proglottids are constantly being produced by a region just behind the head, which is a small round structure studded with anchoring hooks and suckers. As new proglottids form, the older ones are pushed toward the rear, constantly increasing in size.

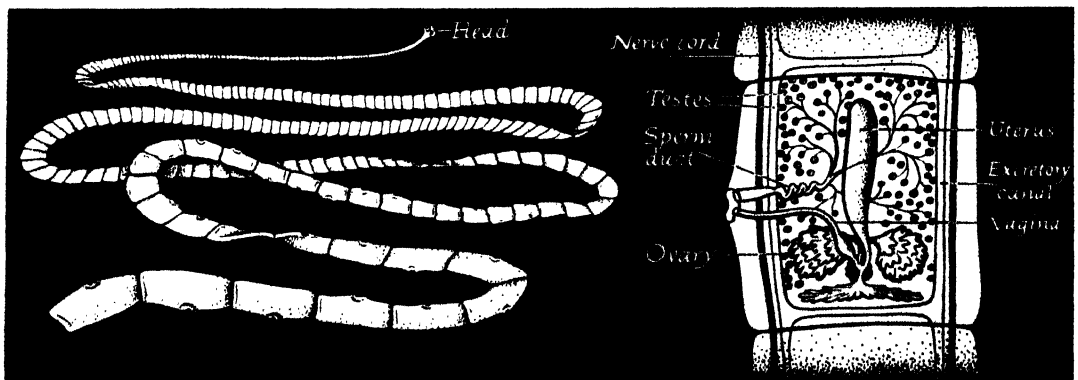
Although the proglottids are hermaphroditic, the male structures deteriorate before eggs in the female structures mature, and the older ones are fertilized by sperm from the younger. The young proglottid in its male phase has a muscular penis with which sperm is introduced into the vagina of an older proglottid in its female phase, as the worm is looped back and forth in the intestine of the host. Self-fertilization is general, though cross-fertilization may take place if several worms occupy the same host. Eventually the proglottids, crammed with fertilized eggs, separate from their tape-like parent and are eliminated with the host's feces.

The small hooked embryos which develop must be ingested by a secondary host of a dif-

ferent species in order to mature. In this secondary host the hooked larva bores through the intestinal wall, is picked up by the blood stream, and is carried to all parts of the host's body. Depending on the kind of tapeworm, the larva now lodges in muscles or in other tissues and forms a bladder (*cysticercus*) within which the inverted head of a new tapeworm forms. Here it remains until the host dies, and generally the cycle is not completed unless the *cysticercus* is eaten by a specimen of the primary or original host species. Once more in a digestive tract, the bladder is dissolved by the digestive juices and the head of the new worm is liberated, anchors itself by means of hooks and suckers, and starts to grow a new chain of proglottids (Fig. 252).

The reproductive cycle just described is representative of tapeworms in general and is precisely that of the beef tapeworm (*Taenia saginata*). For this species the primary host is man, for it is within his intestinal tract that the long string of proglottids is produced. If the eggs are eaten by cattle, the bladder-like cysts develop in the muscles of this secondary host. Infected beef, if insufficiently cooked, may thus produce a crop of tapeworms in the human intestine. For the pork tapeworm (*Taenia solium*) man is again the primary host, but the pig is the usual secondary host. An added danger from this cestode lies in the possibility of self-infection by the ingestion of eggs through unclean personal habits. Whenever this happens, the bladder-worms develop in the human

Fig. 251. The beef tapeworm, *Taenia saginata*, and an enlarged view of one of its proglottids, consisting almost entirely of reproductive structures.



host instead of in the pig — sometimes in vital organs, as in the brain. Another cestode of special concern to man, *Echinococcus granulosus*, differs in that man is a secondary while the dog is usually the primary host. Since the mature worm does not exceed a quarter inch in length, it is surprising that the multiple cysts are sometimes larger than a grapefruit, often forming in the victim's liver or sometimes in the brain. Human beings may become infected from an infected dog, and careless contact with dogs, such as permitting one's face to be licked, increases the danger.

THE PROBOSCIS WORMS: TWO NEW DEVELOPMENTS

The marine worms formally known as the *Nemertea* (Gr. *nemertes* = the unerring Nereid) have many characteristics in common with flatworms. Nemertians are long, ribbon-like, fragile creatures, entirely covered with cilia, often brilliantly colored, and equipped with a proboscis, a long muscular tube which can be shot out to grasp prey. Like many flatworms, they have a mesoderm and an excretory system consisting of ciliated flame cells and canals. But they also possess features not shared by the flatworms nor found anywhere below them, certain evolutionary "firsts."

Instead of having a sac-like gastro-vascular cavity, they have a tubular alimentary tract, with the mouth at one end and an anus at the other, for the first time utilizing a flow-through system with all the potentialities for specialization and efficiency of a modern assembly line. They also have a blood-vascular system and blood with the same red oxygen-carrying hemoglobin as in many higher organisms, including man. Thus undigested and partly digested food is carried to the body tissues not by a branched digestive tract, as in flatworms, but by a distributing fluid through a special system of tubes. Extremely primitive in the nemerteans, this system is greatly elaborated in all but degenerate types among higher animals. The nemertine blood-vascular system consists of but three parallel longitudinal vessels, unbranched throughout. There is no special

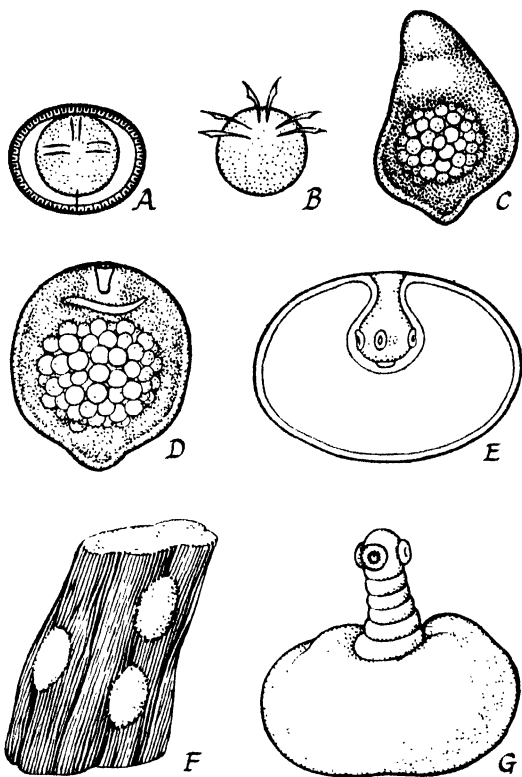


Fig. 252. Stages in the life history of the beef tapeworm *Taenia saginalis*. *A.* An egg containing an embryo with six hooks. *B.* Freed larva in digestive tract of cattle. *C.* Young larva (*cysticercus*) from muscle tissue of infected cattle. *D.* Later stage of the larva showing the invagination of the head. *E.* Diagram of the larva at later stage, showing the invaginated head. *F.* Section of "measly beef" showing imbedded larvae. *G.* Early stage of a tapeworm in the intestine of man. The head, with suckers, is everted and proglottids are forming.

pumping mechanism, the blood being simply squeezed along by the muscular contractions of the body. These same body movements also propel the contents of the alimentary canal from mouth to anus. It is important to note that the larva of the proboscis worm is similar to the trochophore larva and relates it to the higher phyla of the annelids and the mollusks.

THE ROUNDWORMS OR THREADWORMS

Commonly known as roundworms or threadworms, the unsegmented worms of the phylum *Nematoda* (Gr. *nema* = thread) are legion. They are found free-living in vast numbers almost everywhere and under almost all condi-



Fig. 253. *Ascaris lumbricoides*, an intestinal parasite frequently found in man.

tions. A cupful of soil may contain over 100,000 of them. Some are highly and amazingly specialized and are found only under narrowly limited conditions, as the vinegar eel, which lives in vinegar. And one species has never been found anywhere except in the felt mats placed under beer mugs in Germany. Some of them are human parasites, such as the hookworm, the common intestinal pinworm, the trichina worm, and the filarias of the tropics, which cause filariasis and elephantiasis. While most roundworms are about the size of a piece of thread, the guinea worm, which causes abscesses in the connective tissue under the skin of man, grows over a yard in length and is extracted by slowly winding it on a stick. Indeed, there are few plants or animals quite free of parasitic nematodes.

General Characteristics

Structurally, most roundworms are much alike. They are thread-like and tapered at either end. The body is covered by a tough cuticle secreted by the ectoderm. There are no cilia, and they move by means of longitudinal strips of muscle which enable them to bend or whip about. But since there are no circular muscles, there is no change in length or thickness and no real crawling.

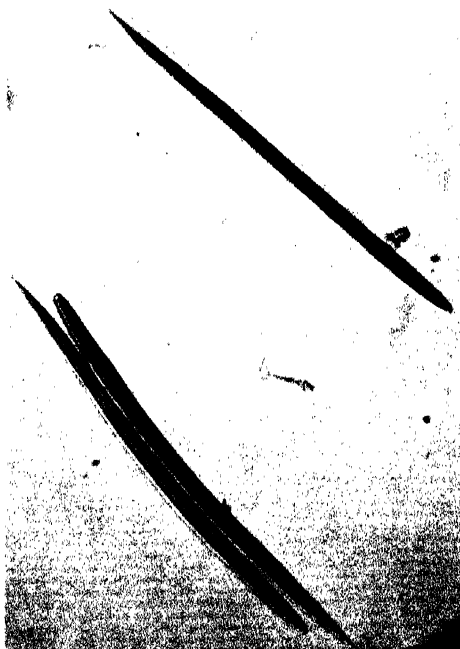
The tubular intestine has mouth and anus, as in the nemertine worms, and consists of a single layer of endodermal cells. Giant cells within the primitive body cavity are reminiscent of the mesenchyme of the flatworms. A marked difference from the flatworms, however, is that there are two nerve-cords, one

dorsal and one ventral. The primitive body cavity within which the intestine lies produces for the first time a suggestion of the "tube-within-a-tube" system characteristic of all higher animals. In most nematodes the sexes are separate, as in nearly all the higher animals. While the group is primitive in many ways, it shows several important evolutionary advances.

Parasitic Roundworms

While most roundworms are free-living, the parasites among them are widespread and create immense havoc. Their odysseys through

Fig. 254. Hookworm larvae from soil. These drill through the skin and enter the circulatory system.



the human body in the completion of their life cycle are of great biological interest.

Ascaris. Chief among those which infect man as well as other animals are the ascarids, the most common intestinal worms. These include *Ascaris lumbricoides* (Fig. 253) and the common pinworm *Oxyuris vermicularis*. The life history of these creatures is relatively simple, but it includes some amazing detours within the human body. Eggs are discharged with the feces of an infected person. Careless habits, especially prevalent among children, sometimes result in the swallowing of the eggs. In the intestine, the young worms within the egg case are released through action of the digestive juices. They burrow through the intestinal wall into the lymph vessels and thence into the veins, pass through the heart and into the lungs, where they penetrate the delicate air sacs and reach the lung cavity. From there they go up the trachea into the throat, only to be swallowed again. Once more in the intestine, they reach maturity by sharing the digested food of the host, causing general debility and intestinal pain. In the intestine they lay their eggs — a single female may lay as many as 200,000 daily — and start the cycle again.

Similar astonishing cycles are found in other nematodes. No doubt if it were known, the whole evolutionary history of these organisms would explain the origin of that strange wanderlust that incites the larval worm to the preliminary exploration of his universe before finally settling down to reproduction.

Hookworm. Small in size but devastating in effect is the common hookworm, *Necator americanus* (L. *necare* = to kill). The adult worm lives in the human intestine, where it clings to the intestinal wall with its mouth, sucking blood and other tissue fluids. As in the ascarids, the eggs pass to the outside world with the feces, but they hatch on the ground and soon grow to a stage where they are ready to seek a new host (Fig. 254). When human skin — usually that of a bare foot — comes in contact with infested soil, the little hookworm penetrates it and drills through to the blood stream. It then follows the same course as *Ascaris* and

finally lodges in the intestine, to complete the cycle. Since a young hookworm is active only in warm soil, this parasite is limited to tropical and semi-tropical regions. Infected individuals develop marked symptoms — in children, retardation of physical and mental development; in adults, anemia and lassitude. Millions of our own citizens in southern states are still victims of this parasite.

Trichina. A third nematode parasite is the trichina worm, *Trichinella spiralis*. Trichinosis, the disease caused by this organism, is far more common than is usually suspected, since a light infection may not be serious in its results. Infection results from eating meat, most frequently pork, that harbors living encysted young worms (Fig. 255). Since the cysts are only about $\frac{1}{16}$ inch long, only micro-

Fig. 255. Cyst of trichina (*Trichinella spiralis*) in human muscle. The cyst in itself is harmless and the worm dies unless eaten in time by another host. Damage to the host arises from mass migration of millions of worms to their encysting place.



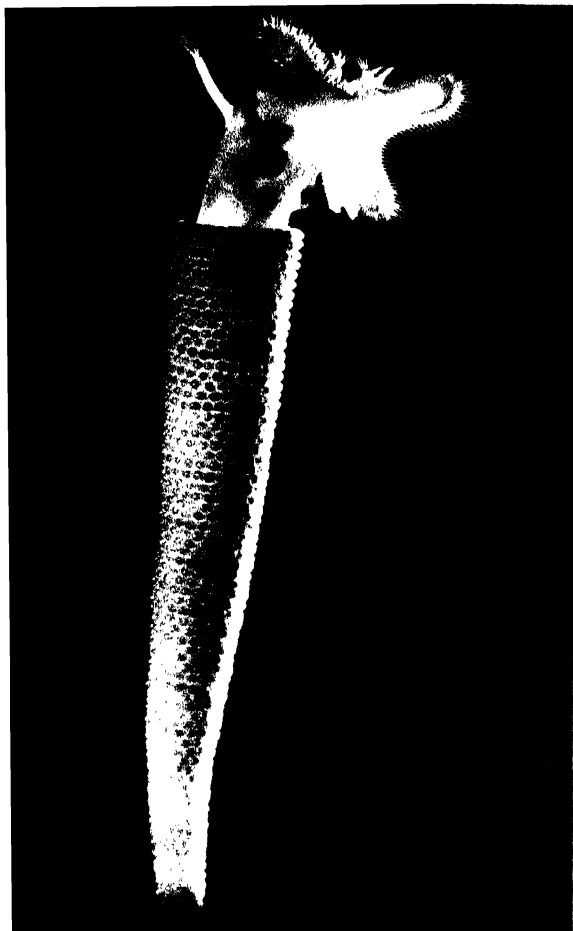


Fig. 256. Glass model of *Melicerta ringens*, a tube-dwelling rotifer. The tube consists of pellets of carefully molded fecal matter.

scopic examination reveals their presence where infestation is light. In heavy infestation, hundreds of thousands of encysted worms may be found in a few ounces of meat. The larva of the trichina worm develops within the human host and burrows into various organs and tissues, especially the muscles, including those of the eyes and the tongue. Anemia, fever, stiffness, swellings, and even delirium are common symptoms. In extreme cases, as many as 500 million larvae may be present in the host at one time. Thirty per cent of the severe infections result in death, since after the migration has begun, there is no means of stopping it. There is thus real and terrible reason why pork should be thoroughly cooked.

Although the nematodes are important to us mainly as parasites, most of them are free-living, and they have made the evolutionary contribution of separate sexes, a condition found in most higher animals.

THE ROTIFERS OR WHEEL ANIMALCULES

These ubiquitous little creatures are known to everyone who has ever peered through a microscope at a drop of water from pond, puddle, or stream. Smaller than many a protozoan, they are nonetheless rather highly organized metazoans. Their peculiar ability to withstand drying out has made them cosmopolites, for they are sometimes carried from land to land by birds and wind, and they survive even in a dry condition. The rotifers show the greatest diversity of form and habit, although in basic plan they are much alike. Some, like *Trochosphaera* (Fig. 257), are spherical. Others are worm-like in shape. Some live in tubes which they have made of gelatinous materials, cemented debris, or of their own pill-like fecal matter (Fig. 256). *Melicerta ringens*, for instance, possesses a special glandular shaping-organ in which it molds its feces into perfect little spheres before using it as building material.

Diverse as they are in form, they are no less so in living habits, for they have been found in fresh, brackish, and salt water, frozen in arctic ice, and disporting in hot springs.

Although they average only .25 mm. in length, the rotifers are metazoans consisting of about a thousand cells. Moreover, their structure follows a strict pattern, since the number of cells of which their organs are composed is constant within a species. (This is also true of other "worms," such as the ascariids.) Strictly speaking, rotifers are cellular only in their earlier stages. In maturity the cell membranes within their tissues break down, thus forming a syncytium, or non-cellular mass with many nuclei. The nuclei of the syncytia, however, occupy specific positions which normally do not vary.

The organ systems of the rotifer are complex considering the size of the animal. There is

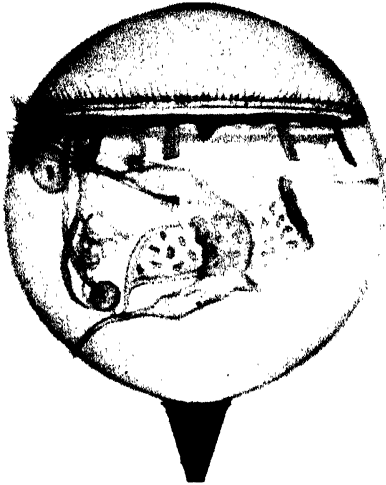


Fig. 257. Glass model of *Trochosphaera solstitialis*, a floating rotifer.

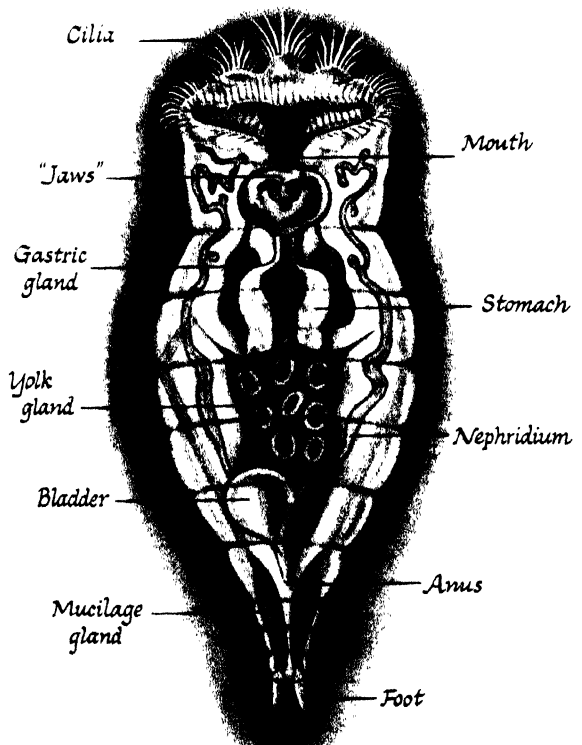
a tubular digestive tract with mouth and anus. The mouth is surrounded by various arrangements of beating cilia which give the class its name (Gr. *trochos* = wheel), for their motion has the appearance of a turning cogwheel. Currents of water created by their beating sweep food into the mouth, and the particles then swallowed pass between the "jaws" of a chewing mill, the *mastax* (Fig. 258), which may easily be mistaken for a beating heart. Food passes to a stomach-like digestive sac, while a rudimentary intestine carries waste matter to the anus.

A rotifer swims with the aid of its crown of cilia, or crawls in the fashion of an inchworm. Many rotifers have a pincer-like foot, often equipped with mucilage glands, useful for holding themselves attached to a plant or rock while they feed. A system of excretory flame cells empties through tubes into the lower intestine. Coordination is unusually precise for so small an organism. While the animal is attached to some support, there is a constant and apparently purposeful circular motion in its crown of cilia, which beat rhythmically in a progressive wave around the perimeter of the head. Even more striking is the telescopic nature of body movements in the rotifers, for

both tail and head may be pulled into the barrel-shaped mid-region. As the animal crawls along a supporting surface by alternately humping and stretching its body, its pincer-like toes tap about, almost like the cane of a blind man, seeking a foothold for the next step. All this is directed by a well-developed nervous system which consists of a large ganglion or collection of nerve-cells which may be called a brain. This is located in the head, and nerve branches radiate from it to the various organs of the body. In addition to a sense of touch and a chemical sense, some rotifers possess primitive eyes. Despite their minute size, these smallest of metazoans are more complex than the flatworms.

In the rotifers, like the roundworms, the sexes are separate, but the males, when present, are small and often degenerate. This introduces a new pattern in the evolution of reproduction. In favorable times, the female produces *parthenogenetic* eggs, that is, eggs that require no fertilization by sperm cells. These

Fig. 258. Complexity of the rotifers is shown by this sectional drawing of *Hydatina senta*, a free-living form.



eggs again produce females, so that there is an unbroken line of females throughout most of the year. In some species, at the approach of inclement seasons, females appear which lay two sorts of eggs that differ in size. The smaller of these develop into tiny males with a digestive tract reduced to a vestigial tissue in which the huge male gonad, the testis, lies imbedded. These dwarf males are equipped with a large copulatory organ, or penis, which may enter the cloaca or penetrate any part of the female's body and introduce sperm cells into her body cavity. In many species no males have ever been discovered. In the others, they are a small minority of the population. The fact that the fertilized eggs are protected by a tough shell and may withstand long periods of cold and drying contributes to the survival of the species under unfavorable conditions.

Larval Affinities

In their organs and organ systems, the rotifers show little that has not been seen in other animals. But in their general structure, especially as exemplified in *Trochosphaera*, the group shows what appears to be more than a superficial resemblance to the larvae of annelids and mollusks, called *trochophores*. These larvae are small, helmet-shaped organisms (Fig. 259), generally with a band of cilia about the mid-region which serve for locomotion and to bring food in toward the mouth. The trochophore has a U-shaped intestine, excretory flame cells, and a clump of cilia at the top springing from sensory cells. While it varies from form to form, its basic organization and general appearance is always much the same — and it is startlingly like *Trochosphaera* both in structure and external characteristics.

Most trochophores soon metamorphose into something else. Some become typical marine worms, such as the long segmented annelid, *Polygordius*. Others (after an intermediate larval stage) become typical mollusks, such as oysters and clams. Similar larvae become flatworms or nemertineans. While it is possible that this similarity among larvae of creatures so different in their adult stages is due to con-

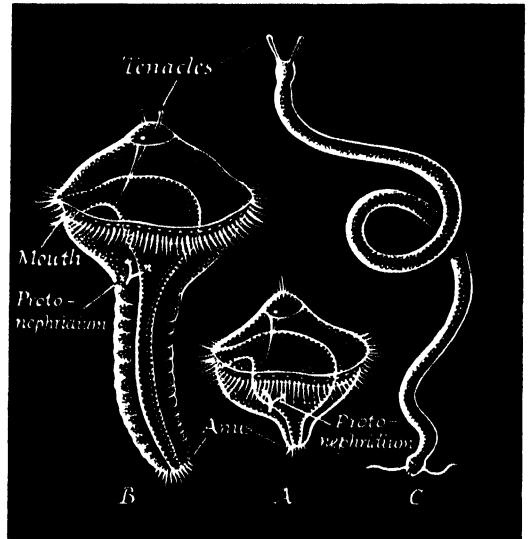


Fig. 259. *Polygordius*, an archiannelid. A and B. Two stages in the development of the trochophore larva. In B the body of the worm is seen growing by the addition of segments to the larva. C. Dorsal view of the adult worm. Compare A and B with *Trochosphaera* (Fig. 257).

vergence, this is not likely, for in the same environment another larval form — that of the echinoderms (the starfishes and their relatives) — is quite different. Rather, the similarity among the trochophores, and their striking resemblance to such rotifers as *Trochosphaera*, is generally interpreted as showing that modern rotifers may be close to the main stem of evolution that produced the flatworms, the annelids, the nemertineans, and the mollusks. Perhaps, indeed, the rotifers can be regarded as a type whose evolution was halted at a sort of larval stage and in that form achieved their sexual maturity, while the other creatures with larvae which resemble them may be more highly developed offshoots of the same basic type.

THE MOSS ANIMALS

Although they contribute no evolutionary advance not seen in other phyla too, the bryozoans (Gr. *bryon* = moss) are highly specialized and rather typical "dead-end" organisms. They are fairly abundant along the seashore, and some species are found in fresh water.

The bryozoans form colonies, which are generally small and vary considerably in form, some being shrub-like and others flat. The colonies are produced by budding from a single individual which is produced sexually. Fresh-water bryozoans form branching growths of gelatinous coverings over sticks in ponds.

Under the microscope the individuals in a colony can be seen unfolding and going about their feeding activities. Few sights are more beautiful. Out of each conical, glass-like tube within which an individual animal lives, and which is really a part of its own body, a U-shaped crown of tentacles slowly unfolds, much like an animated glass flower tinted in pastel colors that range over the entire spectrum. The animal itself is not pigmented, and the color stems from the light interference caused by the thousands of minute cilia that cover its tentacles.

Structure and Behavior

Despite their external resemblance to coelenterate polyps, the bryozoans are far more advanced in internal organization (Fig. 260). The body cavity is a true *coelom*, of the type found in most higher animals, since it is formed in the mesoderm and is completely surrounded by mesodermal tissue. In some varieties, however, this cavity is almost completely filled with a parenchyma in which muscle cells are dispersed. In others, there is a large hollow body cavity into which the tentacle-bearing part of the animal may be retracted. The nervous system is centered in the cerebral ganglion, or brain, as in the rotifers. The excretory system is rudimentary or absent, and there is no respiratory system.

Many bryozoans also show remarkable polymorphism. Some members of the colony alter beyond recognition to become specialized structures, called *avicularia* (L. *avis* = bird) because they are shaped like a bird's head. These apparently prevent other organisms from making their homes on the bryozoan colony, for they have beaks which snap open and grasp intruders.

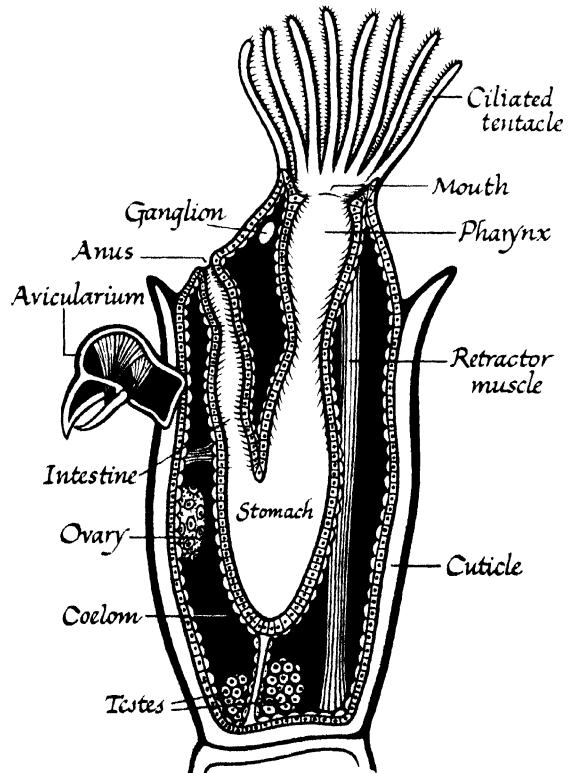
Reproduction is by budding, so long as conditions are favorable. The growth of the colony

is limited, however, for the life span of each individual is short and new individuals no more than replace those that die. New colonies are produced sexually. The animals are hermaphroditic. The eggs are fertilized by sperms inside the coelom. No opening is provided for the escape of the larvae which then develop, and they probably break through the body wall. The larva resembles a trochophore. The colony may also reproduce asexually by budding off internal multicellular structures called *statoblasts*. These are small disks equipped with hooks and capable of floating and able to withstand adverse conditions. Odd mixtures of the advanced and the primitive, the bryozoans are on an evolutionary side track.

THE LAMP-SHELLS

This phylum (*Brachiopoda*) too is of uncertain relationship, but its trochophore-like larva suggests that it is part of the same branch as the "worms" and the moss animals. It is mentioned because it shows in rudimentary form two or-

Fig. 260. Plan of a bryozoan.



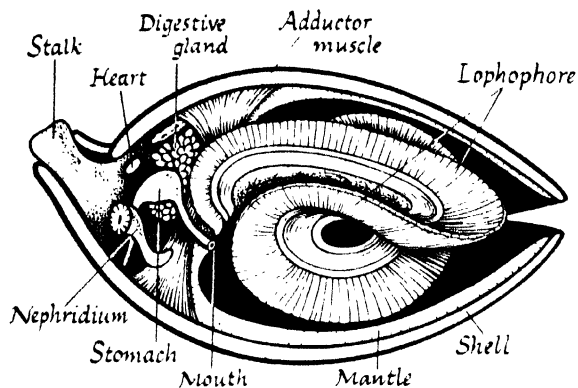


Fig. 261. Sagittal section of a brachiopod.

gans which have not appeared earlier and which are of considerable importance in higher animals — a kidney and a heart. Although they look like mollusks, especially small clams, lampshells have an internal structure that is quite different and somewhat resembles that of a bryozoan. Whereas the shell of a clam consists of right and left halves, that of a brachiopod is dorso-ventrally arranged and opens at the animal's anterior end. Internally, a brachiopod has a pair of large, lobed, ciliated arms, similar in appearance to the crown of tentacles borne by the bryozoan, and serving the same function. The digestive system is tubular, and is separated from the body wall by a coelom, as in some bryozoans. One important innovation is a primitive ciliated kidney, or *nephridium*, which serves for excretion and also permits the larvae, which hatch within the coelom, to escape. This is quite an improvement over the situation in the bryozoans. Another innovation is the simple heart, a hollow muscular organ which circulates the body fluids (Fig. 261). The whole individual is equipped with a stalk by which it attaches itself to a solid support or, in some species, buries itself in a burrow in the sand.

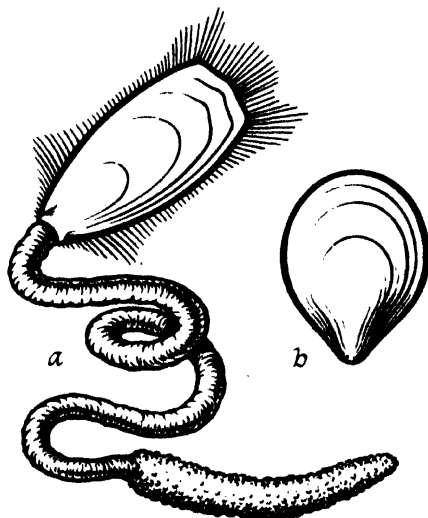
Record of these odd dwellers of the deep goes far back into geologic history. *Lingula* (page 124), a modern brachiopod that lives in sand tubes (Fig. 262), is almost a duplicate of fossil brachiopods that flourished on earth in the lower Cambrian some 500 million years ago, and thus may possibly be the oldest known surviving metazoan. Because of their antiquity

and their wide dispersal in past geologic ages, brachiopods are key organisms in determining the age of geologic strata.

THE SEGMENTED WORMS

Typically "worm-like," yet showing a degree of complexity comparable to that of higher animals generally, are the *Annelida* (*L. annellus* = diminutive of ring), which have various numbers of ring-like body sections. It is no overstatement to say that the earthworm, for example, stands higher above the hydra than man above the earthworm. It has climbed its own evolutionary ladder, a different one from ours, but it possesses all the basic structures and systems common to higher animals, including man. Many of these have appeared before, singly, and sometimes combined with others in this group or that, but in no organism as yet studied have they *all* been combined. The annelids have a central nervous system, seen first in the flatworms; a tubular digestive tract, first present in the nemertinean worms; a closed circulatory system, also nemertinean; a true coelom (bryozoan); and a nephridial excretory system (brachiopod). Added to this is a new segmental plan of body structure known as metamerism, evident internally as well as externally. It is no wonder that the

Fig. 262. Brachiopods. A. *Lingula*, a modern brachiopod. B. Fossil of a brachiopod shell from the Cambrian Period. The similarity is striking.



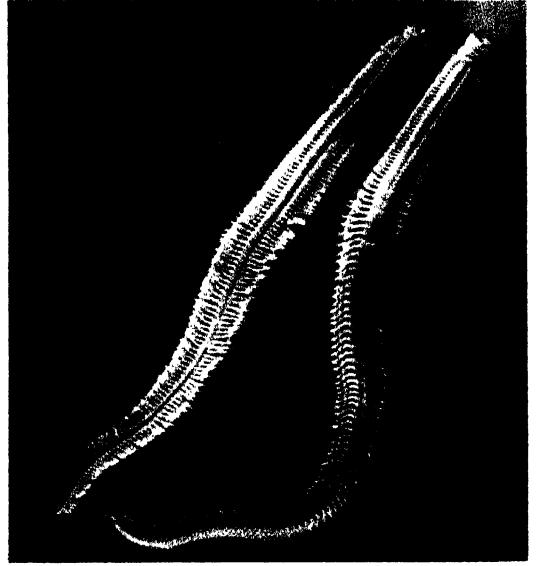
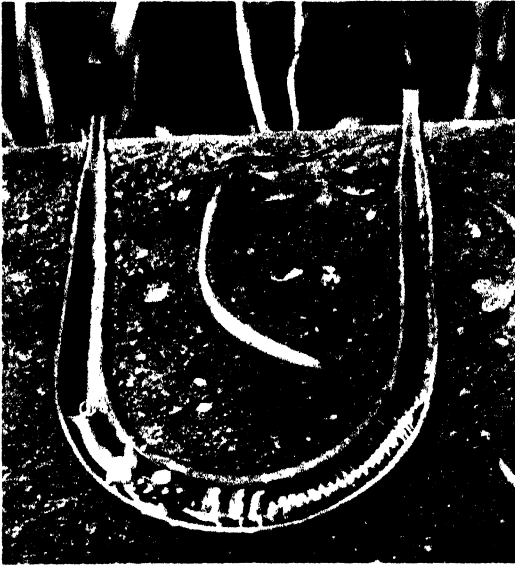


Fig. 263. Three polychaete annelids. *A. Chaetopterus*, a tube dweller, fits perfectly into its secreted tube, which it never leaves. Food is obtained from the current of water it pumps through the tube by piston-like parapods. The worm is luminous. *B. Nereis*, the clam-worm, a good swimmer, though it spends most of its time in its sand burrow. *C. Bispira*, the fanworm, lives in a long tube which it secretes. The anterior end of the worm is adorned with gaily colored, feathery gills which serve for respiration and the ensnaring of food. The speed with which the animal withdraws into the tube belies the flower-like appearance.

annelids are looked upon as a milestone.

Annelids are long and spindle-shaped, with a distinct head end and bilateral symmetry. That their basic pattern is sound and successful is apparent from their great numbers the world over, and from their impressive variety and modification of form. Annelids range in size from the minute *Chaetogaster*, a few millimeters in length, to the giant earthworms of Australia, which may be eleven feet long. In form they vary from the slug-like sea-mouse to flower-like feather-worms and fan-worms, and some of them show distinctive features so prominent as to obscure certain basic characteristics of the group.

Kinds of Annelids

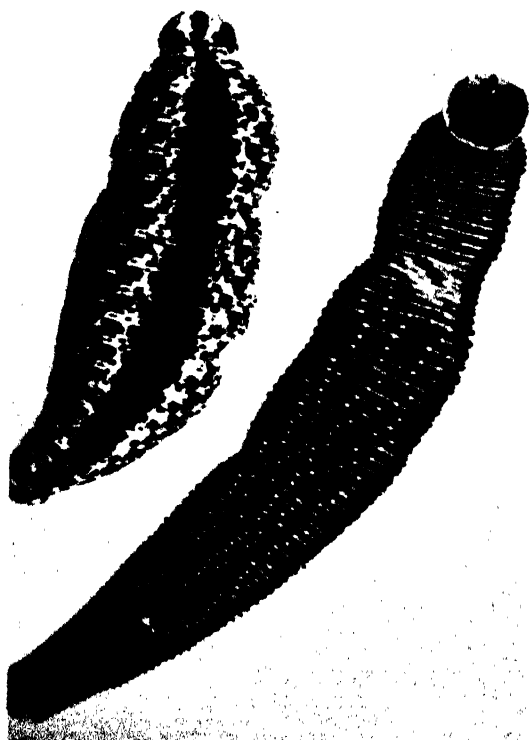
In appearance, the simplest annelids are those of the class *Archannelida* (Gr. *archi* = first), so called because these were long thought to be the parent stock from which more complex annelids derived. These creatures lack the bristle-like appendages characteristic of the largest annelid groups, and do not externally



show body segments. Many of them have cilia, however, like the trochophore larva common to the annelids. It is now generally thought that these are not truly "arch" annelids at all, but degenerate ones (Fig. 259).

A much larger and vastly more important type is the class *Chaetopoda* (Gr. *chaite* = hair). These annelids have bristle-like appendages and are typically segmented but otherwise vary greatly in appearance. Depending on whether they have few or many bristles, they are called oligochaetes (Gr. *oligos* = few) or polychaetes (Gr. *polys* = many). Most oligochaetes dwell in moist earth and fresh water, are less highly developed than the polychaetes, and lack certain structures these possess, such as well-developed eyes, various head appendages including tentacles and gills, and the knobby projections along the sides of the body called *parapods*, from which the bristles arise. The earthworms are representative oligochaetes; typical polychaetes are the sea-mouse and the clamworm (Fig. 263).

Fig. 264. *Hirudo medicinalis*, the medicinal leech, once used in blood-letting.



A smaller group is that of the leeches, class *Hirudinia* (Gr. *hirudo* = leech), which have neither bristles nor parapods, but have a sucker at either end, the mouth being at the center of the anterior one. Most leeches are at least partly parasitic. Like other annelids, they are segmented, but the segmentation is unusual in two ways. They have a limited number of segments — thirty-four. And externally each segment looks like several. The medical leech (*Hirudo medicinalis*), once of prime importance in the medical treatment known as "bleeding," can still be obtained in some old-fashioned drugstores (Fig. 264).

A fourth group of annelids, the class *Gephyrea* (Gr. *gephyra* = bridge), is named for the old belief that these creatures represented a bridge between annelids and echinoderms. They are now generally considered to be degenerate annelids. Sac-like creatures such as *Bonellia viridis*, they live in burrows in the sand and mud at the bottom of the ocean. They begin as trochophore larvae but change into segmented embryonic worms, somewhat after the manner of *Polygordius*. Coelom and segmentation later disappear. *Bonellia* is famous for its manner of sex determination. If a larva finds a mature female which is still unmated, the larva enters her proboscis, penetrates to her uterus, and there changes to a wee parasitic male, living solely to fertilize her eggs on the spot. But if the wandering larva fails to find a female when it is ready to settle down, it grows into a female itself (Fig. 265).

Lumbricus, the Earthworm

Although in some ways not a typical annelid because it lives under ground, the earthworm, *Lumbricus*, shows most of the basic features of the group. Defenseless above ground, it is well adapted for its life of burrowing in the soil. A sensitive lip, the *prostomium*, guides its digging and feeding activities, and it seldom ventures above the surface except at night. Even then, while feeding on decomposing vegetable matter such as dead leaves, it usually anchors its tail in the top of its burrow by means of the short bristles (*setae*) on its ventral surface and seldom

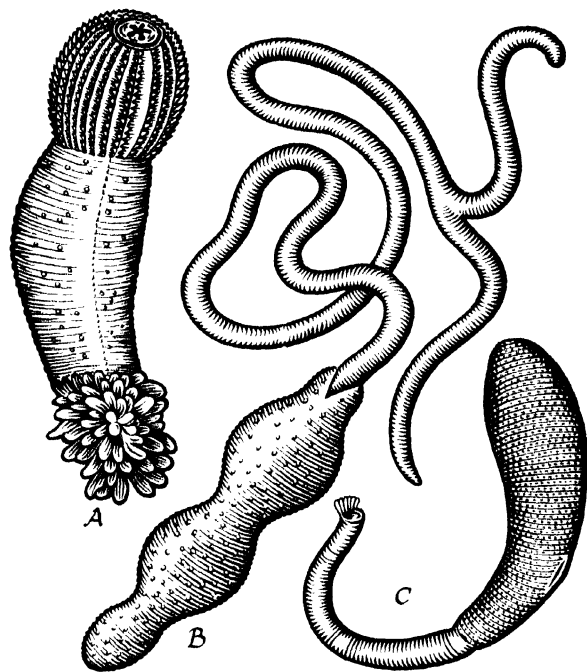


Fig. 265. Gephyrean annelids. Segmented in the larval stage, these worms lose segmentation and coelom as adults. A. *Priapulid caudatus*. B. *Bonellia viridis*. C. *Phascolosoma vulgare*.

wanders farther than it can reach. The hooking action of the setae, together with the curious ability of the worm to flatten its tail and so increase traction, explains the stout resistance it can offer in a tug-of-war with a robin. But it is only the late worm that the robin catches. Tuned to the cycle of night and day, the earthworm is sensitive to light at either end of its body, although it has no true eyes, and generally it retreats into its hole with the first sign of morning.

The appearance of the earthworm gives but little hint of its inner complexity (Fig. 266). The body, composed of a hundred or more segments, tapers toward each end, and a smooth saddle-shaped structure, the *clitellum*, covers segments 32 to 37, counting from the head end.

Fig. 266. The earthworm, *Lumbricus*.



With a hand lens the mouth is easily visible, though somewhat hidden by the overhanging upper lip (prostomium). The openings to the sex organs are minute and hard to find. There are four double rows of setae, easily felt by running the fingers along the worm, and just beside the more ventral rows, on either side, is a row of tiny openings from the *nephridia*, or excretory tubules.

Metamerism. Of the organisms so far studied only the tapeworms show a repetitive pattern, although their "segments" develop by a sort of budding process and are essentially separate individuals. In the annelids, however, each segment, or *metamere*, is permanent and essential, and each is much like every other, including the organs and tissues in it (Fig. 267). Internally the segments are separated by fibrous walls (septa) which divide the body cavity into compartments. Since all the higher animals except the mollusks are built on the metameric plan, it must have brought very great advantages. As we shall see, its one tremendous advantage is versatility. For again and again in evolution whole segments or groups of segments have been completely reshaped in the formation of special organs such as jaw, skull, leg, or trunk, sometimes to a degree that quite obscures the original metameric plan.¹ In the vertebrates the basic segmentation is so overlaid with secondary modifications that it is no longer clearly apparent except in the embryo and the skeleton. In annelids, however, it appears in its clearest, simplest form.

Tissue Layers. Not only in its segmentation, but also in the tissues composing its body, the earthworm is far more complex than any of the animals so far considered. Below the non-cellular protective cuticle lies the epidermis, a single layer of cells, including some glandular ones which secrete the mucus that always

¹ See, for example, the relationship between the various appendages of the lobster, page 111.

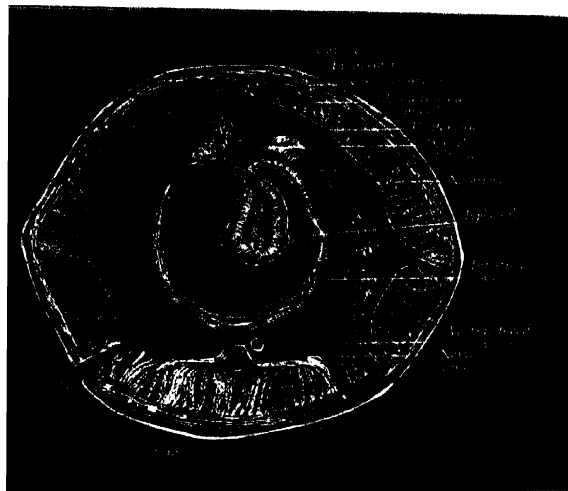


Fig. 267. Cross-section of *Lumbricus*, somewhat diagrammatic.

covers the body of the worm. Next is a layer of circular muscle fibers, and below this is a heavier layer of longitudinal ones. Finally, in the body wall, is a thin layer of flat mesoderm cells lining the coelom or body cavity (Fig. 267).

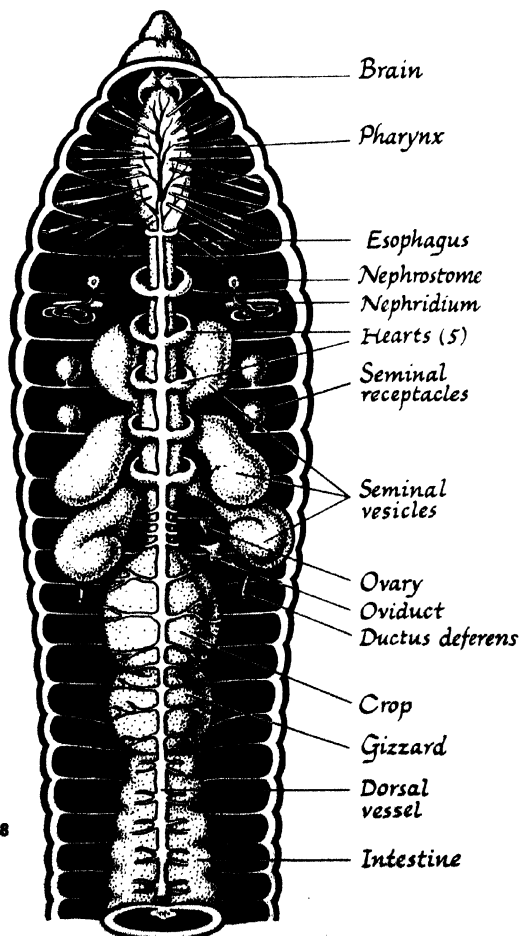
But this is not all. The digestive tube, which runs the full length of the body, is covered by a mass of loosely packed gourd-shaped *chlorogen cells*. Then come two thin layers of muscle fiber, first the longitudinal and then the circular, and this time the latter are the larger and stronger ones. These serve to propel the contents through the intestines. The intestinal lining is an epithelial layer of digestive cells, which secrete enzymes and absorb food. Compared to *Planaria* the earthworm indeed has a complex arrangement. Its coelom is well developed, and the tube-within-a-tube body plan has gone far along the evolutionary road.

Movement. The earthworm hitches itself forward by stretching its body, hooking its forward setae into the ground, and pulling the rest of itself forward by contracting the longitudinal muscles in its body wall. The angle of the setae can be reversed by small muscle fibers attached to their inner ends, and hence the worm can crawl in either direction. Indeed, it sometimes pulls itself back out of harm's way with astonishing speed.

Digestion. The tubular digestive tract with openings at each end is a distinct advance over

the simple gastro-vascular cavity in one striking way: it offers a chance for increased specialization. In the earthworm this surpasses considerably the amount to be found in nematodes or other forms already considered. The mouth opens into a large muscular sac, the pharynx (Fig. 268), which like a rubber bulb on a medicine dropper sucks in bits of organic matter held to the mouth opening by the protruding lip. The food is then forced down the digestive tract by muscular contractions of the tube-like esophagus to a thin-walled, bladder-like expansion, the crop, in which it can be stored. It then passes into the thick-walled gizzard, where muscular contraction, aided by the abrasive action of ingested sand particles, grinds up the

Fig. 268. Dissection of *Lumbricus*, simplified. Only one pair of segmental nephridia is shown.



food. Digestion begins in the intestine, which continues undifferentiated to the anus. The *typhlosole*, a longitudinal fold in the dorsal wall of the intestine, increases the secreting and absorbing area.

Circulation. The earthworm has most of the basic features of the circulatory systems of all higher animals — blood, a liquid plasma carrying special blood cells, a closed double system of vessels, arteries which distribute blood to the microscopic capillaries, and veins which collect it again; and a muscular pumping unit (Fig. 269).

The blood of the earthworm is very similar to our own. The same red protein, hemoglobin, carries oxygen; but in the earthworm, the hemoglobin is dissolved in the blood plasma, whereas in most higher animals it is contained within special red blood cells. The colorless, amoeboid blood cells of the earthworm, like our leukocytes, ingest fragments of dead cells, possibly disease-producing bacteria, and certain insoluble foods such as fats, so that they may be transported.

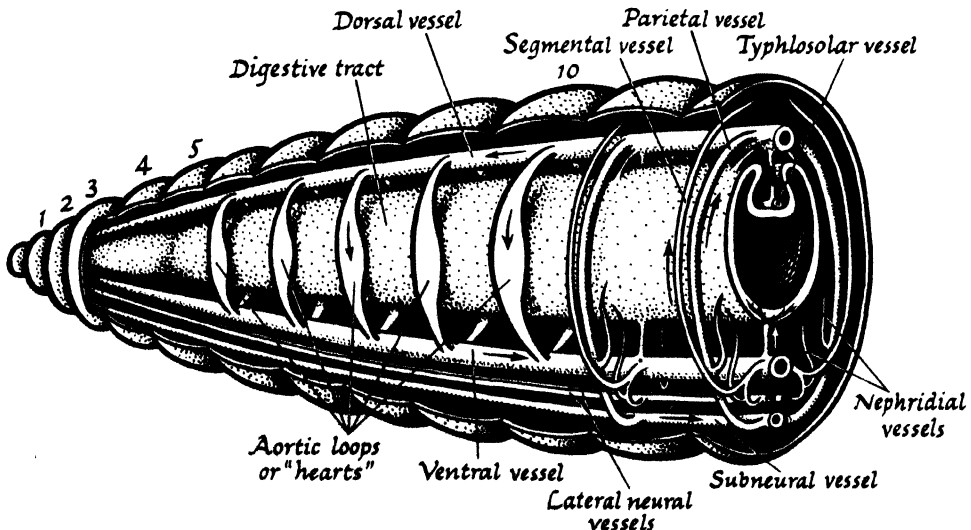
Running up the back of a living earthworm is a pulsating, purplish line, now brighter and now dimmer. This is the dorsal blood vessel, the main one of the system, which moves the blood forward in waves by successive contractions of its muscular wall. Near the head end

five pairs of loop-like vessels with valves branch from the dorsal vessel to join the ventral blood vessel, which runs back along the digestive tract. These loops are the aortic arches or "hearts," and the lower vessel sends branches to the main organs, especially to the digestive tract, nephridia, muscles, and skin.

Simple as this system is, it is yet a vast improvement over any distributing system previously described. Not only are the two functions of digestion and distribution separated in the earthworm, but the blood is pumped around a definite circuit, doing its various jobs as it goes — picking up food in the intestine, dropping soluble wastes in the kidneys, and taking in oxygen and giving off carbon dioxide in the skin. Without a vascular system, active animals would probably never have got much bigger than a planarian. For an organism in which distribution is by diffusion alone must be limited in size, and smallness in turn definitely limits the organism's control over its environment.

Excretion. The blood picks up wastes in every organ and tissue and carries them to the nephridia, minute coiled tubes, each beginning in a funnel that opens into the coelom (Fig. 270). The cilia around the opening draw coelomic fluid, containing wastes from the cells, into the tubule. The latter has a rich blood

Fig. 269. The circulatory system of *Lumbricus*; anterior portion in perspective.



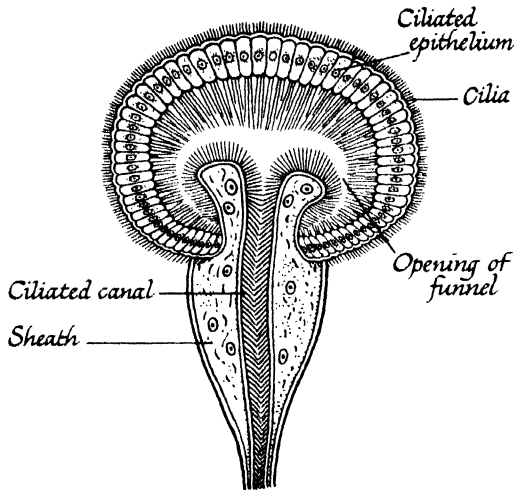


Fig. 270. The nephrostome of *Lumbricus*.

supply through a network of capillaries. Further wastes are secreted into the tubules from the blood, and water and useful substances are probably reabsorbed into the blood stream, as in higher animals, so that the fluid is kept fairly uniform in consistency. The liquids in the tubule, loaded with wastes, then pass into a small bladder which opens to the outside. The typical earthworm nephridium is quite similar in plan to the basic excretory unit in the kidneys of higher organisms.

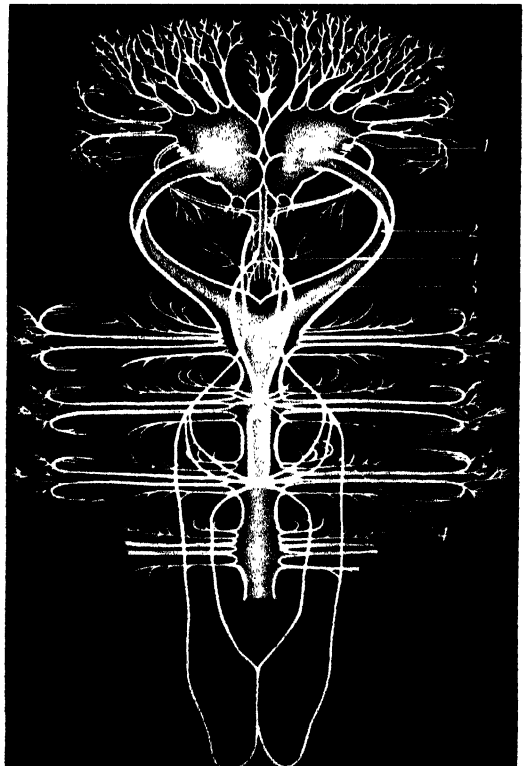
Respiration. The earthworm still “breathes” through its skin. It is thus imperfectly adapted to land life and is restricted to dark moist places. Not all annelids are so primitive, however. The sessile fan-worms (Fig. 263) have crowns of feathery gills surrounding their heads. These make it possible to get enough oxygen even though the rest of the animal’s body is encased in a tube. In *Nereis*, an active marine polychaete with higher metabolism than an earthworm, the breathing surface is increased by capillary networks on the many parapods. All higher and more active organisms have some such mechanism, either in the form of gills, distributing tubes, or lungs.

The Nervous System. The earthworm has a ventral nerve cord, and there is some cephalization, though less than in active polychaetes such as *Nereis* and forms closely allied to it (see Fig. 271), in which the cerebral ganglion,

or nerve center, is considerably larger than the others. In the earthworm (Fig. 272), a more sluggish creature, the cerebral ganglion is less well developed. Except for the prominent nerve-ring around the pharynx, which connects the cerebral with the subpharyngeal ganglion, the most prominent feature of the nervous system is its segmental nature. (In each segment there is a ganglion with three pairs of nerves radiating to the organs and tissues of that segment.) Coordination between segments is by nerve fibers within the cord.

In the main, each ganglion controls the muscles of its segment by a *reflex arc*, the simplest type of nerve connection (Fig. 273). Sensory cells in the epidermis, upon being stimulated, set up a nerve impulse in a sensory nerve with a long strand reaching into the ganglion. Here contact is made with the branched fibers of motor nerves, which by long strands to muscles

Fig. 271. Anterior portion of nervous system of a free-swimming polychaete, *Eunice sanguinea*. 1. Cerebral ganglion. 2. Circumpharyngeal commissure. 3. Subpharyngeal ganglion. 4. Intestinal nerve complex.



and glands incite them to action. The ganglia are clearly autonomous, for responses still take place within a single segment after it has been disconnected from the rest of the central nervous system. The reflex arc also exists in higher organisms, including man. Intercommunicating fibers between the ganglia of the earthworm also make it possible for stimuli received in one segment to bring responses in others.

Organs of Perception. The earthworm's mode of life has produced some degeneration, especially in the sense organs. For its light receptors — scarcely eyes — consist simply of light-sensitive cells partially shielded by pigment spots which cast a shadow upon them. These structures can merely distinguish between light and dark, and possibly the direction of the light, and are much less efficient than even the eyes of *Planaria* or the coelenterates.

Certain other annelids are much more highly developed in this respect. The active predacious polychaetes, such as *Alcioppe* (Fig. 274), have true eyes. A cup-like infolding of the epidermis has light-sensitive cells equipped with rods similar to those in the human eye, and nerve processes which join to form an optic nerve. Special cells fill the hollow of the cup with a strongly refractory secretion that acts as a lens. Thus a light stimulus that would otherwise be too weak is made to elicit a response. Other polychaetes actually have a spherical lens within the eye-cup.

In addition to sight and touch, annelids also possess a chemical sense, which may be called taste. The earthworm "tastes" with its entire skin, but especially at the head end. Microscopic examination of the epidermis reveals

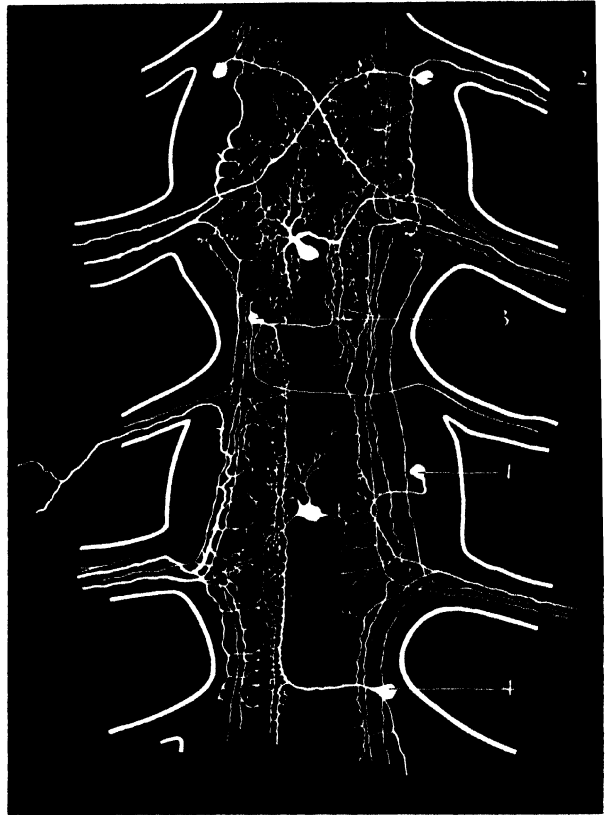
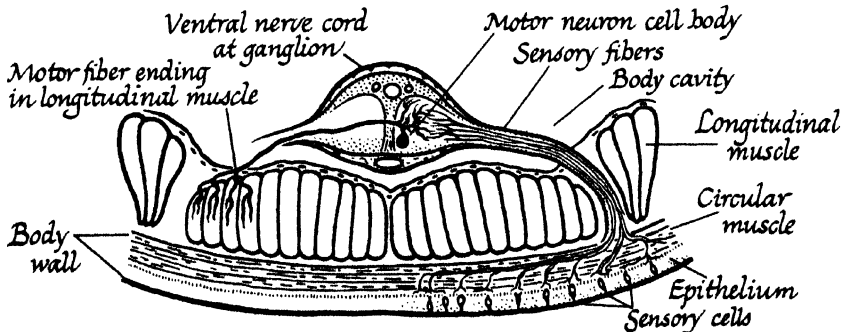


Fig. 273. Two segmental ganglia of *Lumbricus* in which individual neurons have been selectively stained. 1. Neuron sending fibers into a nerve of the same side. 2. Neuron sending fibers into a nerve of the opposite side. 3. Neuron sending fibers into nerve bundles of an adjacent ganglion. 4. Neurons sending fibers into adjacent ganglia only; hence, associating neurons.

peculiar sensory buds with ciliated cells. The anterior segments have almost three times as many of these sensory buds as the middle ones.

Reproduction. Reproduction in the earth-

Fig. 272. Primary sensory and motor neurons of the ventral nerve cord of an earthworm.



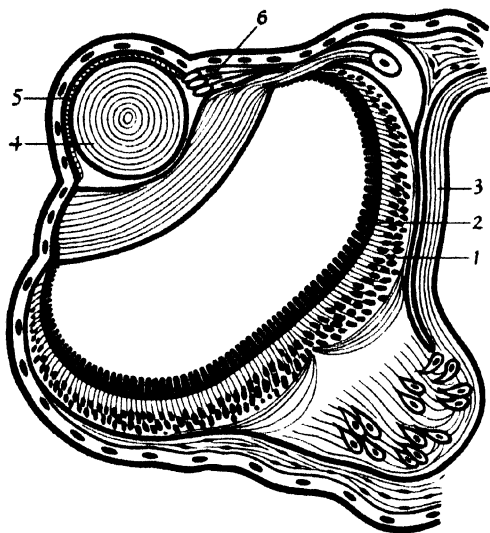
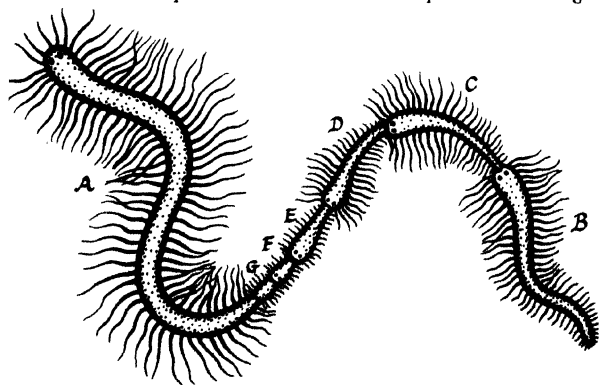


Fig. 274. Highly evolved eye of the polychaete annelid, *Alciope*. 1. Visual cells bordered with pigmented layer. 2. Rod-like processes of visual cells. 3. Optic nerve. 4. Lens. 5. Muscles which flatten corneal dome for accommodation. 6. Accessory retina.

worm is entirely sexual, although some annelids have retained the ability to reproduce asexually. Because the body segments are homologous, some annelids produce whole chains of new individuals by budding at the posterior part of the body (Fig. 275). In some forms the asexual and sexual processes alternate in a pattern somewhat like the alternation of generations. This is true in the famous palolo worm, *Eunice viridis*, of the Samoa and Fiji Islands, which is the chief party in two annual native festivals. In October and again in November of each year, on the day of the last lunar quarter, sexually ripe chains of segments, some male and

Fig. 275. Budding in the polychaete annelid, *Myrianida*. Sequence of letters indicates sequence of budding.



some female, are produced by budding from the adult worms. These are all produced almost simultaneously by the adult *Eunice*, which lives in the crevices of the coral reefs. The segments swim to the surface in huge numbers, where they release their eggs and sperm cells in the water. The spent worm-fragments then sink to the bottom and die. Natives celebrate all night in anticipation of the appearance of the first swarm, which comes with the first graying of dawn. The swarming sexual individuals are caught by the thousands in baskets, and are considered the greatest of delicacies. The adult worms remain in their coral crags and regenerate their missing tail parts.

The earthworm is hermaphroditic. Its reproductive system consists of the primary organs, the *ovaries* (segment 13) and the *testes* (segment 10); secondary female structures, the *egg sac* and the *oviducts*, which convey the eggs to the outside of the body; secondary male structures, the *seminal vesicles*, three large pairs of lobes where sperm cells are stored, and the *vas deferens* or sperm ducts, which carry the sperm cells to the outside; structures which may be considered either male or female, the four *seminal receptacles*, which receive and store sperm cells from another individual. One might suppose each worm able to fertilize its own egg cells, but instead, each worm always mates with another (Fig. 276) and stores the sperm until its own eggs mature. At that time the thick U-shaped structure covering segments 32 to 37, the clitellum, secretes a horny ring that is gradually worked forward. As it passes the openings of the oviducts it picks up eggs, and as it passes the openings of the seminal receptacles, it picks up the sperm derived from the other worm. Fertilization now takes place, the ring continues to the front end, closes up and is released as a small cocoon. The fertilized eggs hatch into small earthworms without going through a larval stage, although a disproportionately large head, equipped with a "head kidney," suggests that a larval stage did occur in a progenitor.

Embryonic Development. The development of the egg into a young worm shows many

fundamental processes characteristic of all higher animals. By a series of mitotic cell divisions, the fertilized egg gives rise to a hollow flattened ball of cells called a *blastula* which corresponds to the final stage in the development of the colonial *Volvox* (see page 173). One cell in the blastula proliferates new cells into the cavity within the ball. This cell, the *primary mesoblast cell*, produces the mesodermal tissue. The cells on one side of the blastula are larger than those on the other. The larger ones begin to flatten out and then to bulge inward, forming a hollow-walled cup, the *gastrula*. At this stage the embryo has assumed a pattern comparable to that of the coelenterates, except that it has a mesodermal layer. The cup-shaped structure stretches, elongates, and begins to take on the shape of a worm. Mouth and anus are formed, and the mesoderm develops the coelomic segmental cavities of the earthworm. Meanwhile a ridge of cells has bulged off from the ectoderm on the ventral side to produce the nerve cord. The essentials of the earthworm have been established. In marine annelids that still live in the environment of their ancestors, the eggs hatch into typical trochophore larvae. The earthworm is unquestionably related to the marine worms in its structure, and its failure to pass through a trochophore stage must be an adaptation to land life made long ago.

The place of the annelids in the evolutionary scale is marked less by new developments than by a combination of developments which have appeared separately in other organisms lower in the scale of life. Bilateral symmetry, cephalization, a centralized nervous system, metamerism, a blood-vascular system, an excretory system, a true coelom, the tube-within-a-tube structure, and a continuous digestive tract — most of these things we have already seen in whole or in part in other animals, but nowhere all together or so completely developed as in the annelids.

THE MOLLUSKS

Veering sharply from what we usually think of as the main line of animal evolution are the



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Fig. 276. Copulating earthworms. Each worm has brought its sperm-duct opening in apposition to the seminal receptacle openings of the partner, thus making possible an exchange of sperm cells. In this manner cross-fertilization is achieved in hermaphroditic animals.

mollusks, phylum *Mollusca* (*L. molluscus* = soft), soft-bodied creatures generally without internal supporting structures and showing little or no trace of segmentation. In many ways the mollusks appear to us to be the strangest creatures of the animal kingdom because their evolution has been so different from ours. Springing, probably, from ancestors common to the other phyla mentioned in this chapter, very likely primitive rotifer-like organisms more highly developed than coelenterates, they have gone a separate way from those descendants of other primitive types which led to the joint-legged invertebrates and culminated in the insects. Yet the mollusks are one of the most varied, complex, and efficient of invertebrate phyla, and it may be for this reason that they have led to no group more highly developed than themselves.

Including such widely different creatures as snails, clams, and octopods, the mollusks range in size from tiny snails less than a millimeter in length to giant squids over fifty feet long, and in form from the sluggish chitons (Fig. 277) to the active and intelligent squids and octopods (Fig. 283). The effectiveness of their basic organization is evident from their wide distribution in many environments. Snails live both

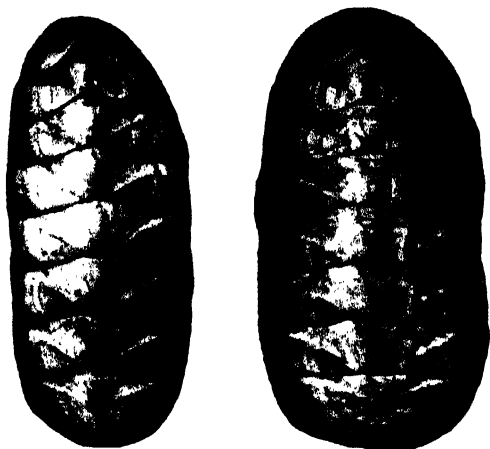


Fig. 277. Chiton, a primitive mollusk. These specimens are from San Pedro, California.

in water and on land; some mussels live in salt water, some in fresh; oysters, clams, and elephant's tusks burrow in the mud and sand of the ocean bottom; sea-slugs float passively in the open ocean; squids and octopods swim actively in the ocean or lurk in rocky crevices. So diverse are the forms in this phylum that some biologists do not consider the mollusks a homogeneous group, though it is generally believed that they represent divergent branches that sprang from a common ancestral stock.

Despite their wide distribution on land, the mollusks are a marine phylum, and their earliest fossil representatives in the lower Cambrian period were sea dwellers. These were simple gastropod types, with little conical shells like those of the limpets of the present day. Some mollusks invaded the fresh water in the Devonian and the land in the Carboniferous, but by far the greatest number are still marine.

Body Plan

The soft body of a mollusk is generally formed of three regions. The ventral portion, into which some of the viscera extend, is enlarged into a lobe-like muscular *foot*. The dorsal portion is extended into two folds, like the flaps of an open jacket, which extend over the foot on either side to form the *mantle*. In all forms except the bivalves (clams, etc.), there is gen-

erally a relatively mobile head equipped with sensory organs. This general body plan has been modified in many ways. Other features characteristic of most, but not all mollusks, are a shell, secreted by the outer portion of the mantle folds, and gills or lungs, developed from modifications of the inner surfaces of these folds. The digestive, excretory, and reproductive systems empty into the coelom, which is much reduced and may be only a small space surrounding the heart. Many mollusks also have a rasping organ or tongue, the *radula*, which is used in feeding. The diversity within the class is very great.

Simple Mollusks: The Amphineura

The mollusks are generally divided into five widely variant classes, of which the most primitive is the *Amphineura* (Gr. *amphi* = double + *neuron* = nerve), in which the central nervous system is still in the form of two double lateral strands, one pair above the other, and there is an articulated shell, usually of eight segments. Two groups, unlike in other respects, are included in this class, the chitons and the solenogasters (Gr. *solen* = channel).

The chitons are oval and flattened creatures generally not more than a few inches in length, and their shells are sometimes beautifully ornamented (Fig. 277). They are bilaterally symmetrical but have none of the twists and turns of the more highly specialized mollusks. Chitons adhere closely to the surface of rocks, where they feed on algae or coelenterate colonies. If disturbed, they can roll up into a ball. Though usually found in shallow water, some species live several miles down.

The solenogasters are worm-like and have no shells. The foot is much reduced or quite absent. Some biologists regard them as more closely related to simple flatworms or annelids than to mollusks, but they do develop from a trochophore type of larva.

Snails and Slugs: Gastropods

More familiar are the snails and slugs, members of the class *Gastropoda* (Gr. *gaster* = belly



Fig. 278. In the land snail (left) a part of the mantle-cavity is transformed into lungs. Slugs (right) are snails in which the shell has been reduced to a thin plate embedded in the mantle. The damp "trails" they leave behind them are made by slime which they secrete as a protection against mechanical injury.

+ *pous* = foot) and aptly named, because in these animals the "belly" has literally been transformed into a foot (Fig. 278). The gastropods differ from other mollusks chiefly in having a one-piece, spirally coiled shell without inner chambers. In some specialized or simplified forms, the shell is present only in the embryonic stages; in others it changes shape as the animal matures. The spiral structure of the body has resulted in the loss of those organs on the left side, so that the creature is no longer bilaterally symmetrical. The body is in three main sections, and the space within the mantle contains gills or lungs. In gastropods that live on land, the mantle cavity is sealed from the outside except for a small breathing pore. The head is usually quite mobile and is equipped with one or two pairs of tentacles, one pair of which may have eyes either at the base or at the tip. Other sense organs are the statocysts or balancing organs, and the olfactory organs. Some gastropods are carnivorous, but most are herbivorous. The radula, a ribbon-shaped "tongue" studded with rows of teeth, is used in rasping food, such as algae, from the rocks. In one species — *Urosalpinx*, the oyster drill

— the radula is used to file through the shells of oysters so that the animal may feed on their flesh.

The Bivalves: Pelecypods

This large and uniform group, the class *Pelecypoda* (Gr. *pelekos* = hatchet), named for the hatchet-shaped foot, is quite distinct from other mollusks. Characterized especially by a two-piece hinged shell, the bivalves include clams, mussels, scallops, oysters, and shipworms. With few exceptions, such as the shipworm *Teredo*, they burrow in sand or mud, or attach themselves with adhesive threads to some firm base. The shipworm bores into wood, upon which it feeds and within which it finds protection. Bivalves are found in fresh water and in the ocean, and are world-wide in distribution. Although no land forms are known, some mussels have lived out of water for over a year.

The Fresh-Water Mussel

Anodonta grandis, the fresh-water mussel, is typical of the class. It looks like the common clam, except that its shell is darkly pigmented on the outer surface. The mussel lives partly

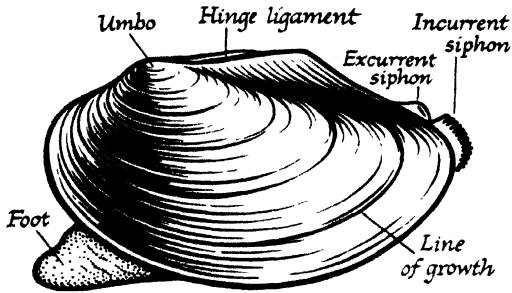


Fig. 279. The fresh-water mussel, *Anodonta grandis*, of the class Pelecypoda.

buried in sand or mud, with the hinge of its shell upward (Fig. 279). It moves by pushing its muscular foot into the sand or mud and swelling the end of it by engorgement with blood. Contraction of the muscles of the foot then pulls against the anchor-like swelling and draws the animal forward. At the opposite or pointed end of the shell are two siphons, tubular openings which can be seen if the animal is left undisturbed. The ventral opening sucks in a current of water and the dorsal one exhales it. If small particles of solid matter, such as chopped food, are dropped in front of the siphons, the particles are sucked into the lower one, and inedible particles reappear at the upper one. If there is too much solid matter in front of the inhalent siphon, the mussel will "cough" violently by suddenly squeezing together its shells. It thus expels the offending substance.

The body of the mussel (Fig. 280) is shaped somewhat like a spoon with the handle pointing down. The "handle" is the ventral section, the foot, within which parts of the coiled intestine may be seen. The larger oval formation above this contains the rest of the internal organs: the paired U-shaped kidneys; between their loops the *vena cava*, the vessel through which blood returns to the auricles, at either side of the *pericardial cavity*, the sole vestige of a coelom in these animals; and above the two auricles, the ventricle, or pumping chamber

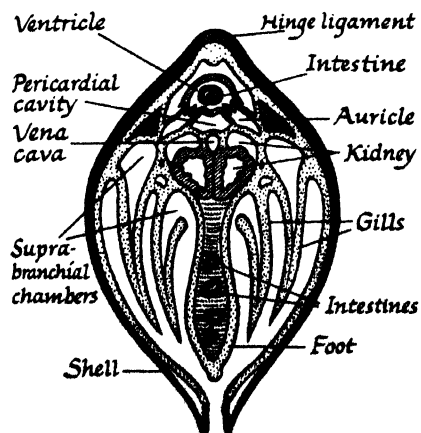
of the heart, oddly pierced by the intestine. The mantle fold extends down either side of the body, lining the two halves of the shell. On its inner surface, the mantle is twice folded to produce *gill plates*, which hang down in the space between the mantle and the foot.

Seen sideways (Fig. 281), the body plan becomes clearer. At the left is the mouth, with two lips or *labial palps*. A short esophagus leads from the mouth to the stomach, which is surrounded by a digestive gland or liver. From here the intestine runs through the foot, pierces the ventricle, and ends in a chamber, the *cloaca*, which opens through the exhalent siphon. In the foot, massed between the loops of the intestine, lie the *gonads*. Cross sections of the large muscles which close the shell are seen posteriorly and anteriorly. A portion of the muscle which aids in retracting the foot is also visible, as are the three ganglia of the nervous system.

How the Mussel Lives

The mussel draws food through its ventral siphon by the action of cilia which cover the gills. Food particles suspended in the water are trapped on the gill surface by mucus, while the water passes on through the fine pores of the gills and is expelled through the dorsal siphon. The cilia propel the mucus-covered food forward toward the ciliated palps, which then transfer it to the mouth. There is no radula in bivalves except for possible traces of one in the young of some species. Enzymes

Fig. 280. Diagrammatic cross-section of a fresh-water mussel.



secreted by the liver into the stomach perform the main work of digestion.

The heart and blood vessels distribute a colorless blood containing amoeboid cells. Other bivalves have red blood containing hemoglobin or blue blood containing *hemocyanin* — a compound in which the molecule contains copper instead of iron, as in hemoglobin. From the heart the blood is pumped through an anterior and a posterior aorta to all parts of the body and is transferred to the veins through spacious cavities or sinuses, instead of capillaries. The bulk of the returning blood passes to the kidneys, where wastes are removed, and from there to the leaf-like gills. Here, as water constantly streams over the large number of blood vessels present, dissolved oxygen in the water and carbon dioxide in the blood are exchanged.

In comparison with more active mollusks, coordination and perception are poor in the mussel. There are three sets of ganglia, one for the foot, one for the “head,” and one for the viscera. Fusion of the first two sets in the head region gives this combined ganglion some prominence over the others, despite the lack of any structure that can be considered a real head. Regions in closest contact with the environment, such as the edges of the siphons and mantle, have scattered sensory cells thought to respond to touch and light. There is also

Fig. 281. Internal organization of a mussel. Mantle and gills of the near side have been removed, and a portion of the body wall has been cut away. Stomach, digestive gland (liver), gonad, pericardium, and kidneys are shown in section.

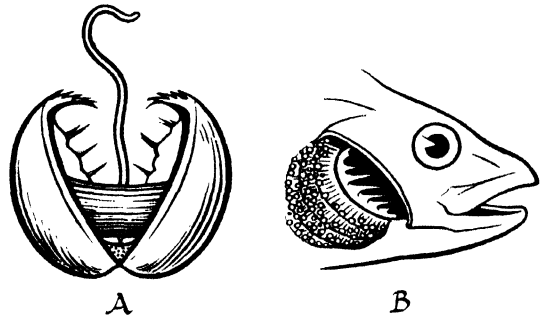
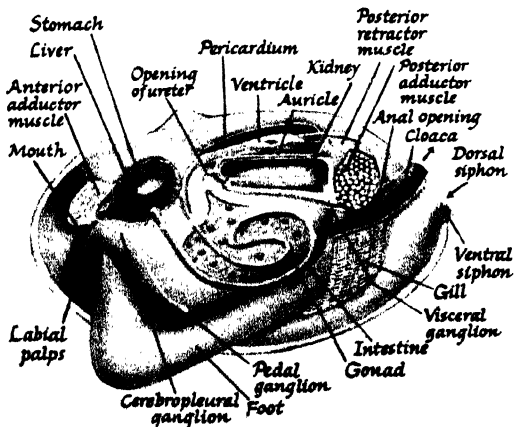


Fig. 282. A. The glochidium larva of a freshwater mussel. B. Glochidia attached to the gills of a fish.

an organ of taste and a statocyst in the foot for balance.

Some bivalves have eyes on their siphons or along the edges of the mantle, the only portions of the body which can be projected beyond the shell. The eyes range from simple light-sensitive cells shielded by pigment spots — no more complex than those of the earthworm — to astonishingly complex organs. Such eyes as those of the common scallop (*Pecten*) have transparent outer protective layers, a lens, a retina, and an insulating pigment layer. The rods of the retinal cells are turned away from the source of light and toward the pigmented bottom of the cup, as in the flatworms, not upward as in the annelids.

Reproduction in the mussel, as in mollusks generally, is sexual, and the sexes are usually separate, though some species are hermaphroditic. As in most mollusks, the fertilized egg develops into a trochophore larva and then goes through a period of growth called the veliger stage before it assumes the form of the adult. In all these respects the mussel is typical. Details of its reproductive cycle, however, are strikingly different.

Sperm cells released into the water by the male are swept into the mantle cavity of the female, where they fertilize the eggs, lodged in special egg cases on the gills. Some three or four hundred thousand eggs are released at one time by the mussel, and in some bivalves an even larger number. Development within



Fig. 283. A highly evolved mollusk, the octopus, one of the most intelligent of invertebrates.

the egg case continues until the larva looks like a peculiar little clam with hinged shells armed with sharp points at their free margin. This is the *glochidium* (Fig. 282). Extending from the center of each larva is a slender sticky thread. By these threads many larvae stick together in clumps, which are ejected into the water only when the maternal mussel is somehow stimulated by the proximity of a fish. For it has been observed that mussels kept in an aquarium have refrained from discharging their young until a fish was put in the tank with them.

The further fate of the glochidia now depends upon the fish. If it swims close enough to a clump so that a thread can adhere to skin or fin, a whole clump of glochidia, snapping their sharp-edged shells like mousetraps, may be dragged along with it, each blindly seeking a firm hold. Those which succeed cause a local irritation and a small blister into which the mussel sinks. The glochidia of some species are picked up by fish in feeding. Most of them are swallowed, but others, as they pass down the throat, attach themselves to the fish's gills, where they undergo the next step in their development. They now feed on the tissues of the fish by means of amoeboid cells, in due time dropping off again to become young mussels. The advantage of this parasitic habit is not very clear, but it has been suggested that it serves to supply the lime needed for early shell growth; and of course the fish in their travels

help to distribute the young mussels widely.

An interesting "revenge" is found in a European dwarf carp, *Rhodeus amarus*. The female of this fish grows a long oviduct which she inserts through the ventral siphon of a mussel, there to deposit her eggs. The eggs cling to the inner folds of the gills of the mussel and there pass through their early developmental stages, eventually to be ejected through the dorsal siphon. Thus host and parasite may quite reverse their roles.

The Cephalopods

The last of the mollusks we shall consider, the octopus, squid, and nautilus, belong to the class *Cephalopoda* (Gr. *kephale* = head + *pous* = foot), so named because their arms — or feet — form a crown about the mouth or head. Marine forms of startling intelligence, the general efficiency of these animals is unmatched in any other invertebrates. Probably around no other animal have more mystery and horror stories been woven than about the octopus or devilfish. This may be ascribed to the fact that these animals combine an anatomy disconcertingly different from that of most others with a pattern of intelligence that closely approaches that of the vertebrates. Cephalopods are widely distributed in all seas and attain the greatest size of any invertebrates. Specimens measuring over fifty feet have been authenticated.

Body Plan. The body reorganization of the squids and their close relatives is quite unlike that of other mollusks, and indeed of other animals generally. First picture a clam lying with its anterior or mouth end toward the left, the hinged portion of the shell (the dorsal side) above, and the foot below (Fig. 284). Now imagine the foot considerably reduced and shifted toward the front, finally growing around the mouth, and then extending outward to form tentacles. At the same time, imagine the dorsal side of the animal to be greatly enlarged, so that it forms a hump-like sac, while the antero-posterior axis of the body becomes greatly shortened. This is the body structure of a cephalopod — much "thicker" than it is long;

for the "length" of the squid is actually the distance from its ventral to its dorsal side. If this seems odd, bear in mind that a somewhat similar reorientation has occurred in monkey and man, where the face is now on a plane with the original ventral surface, and the dorsal side is now posterior.

Anatomy. Aside from this reorientation and the development of tentacles, the cephalopods have a typical molluscan anatomy, though with minor variations. The mantle fold is completely closed except at the anterior end. As in gastropods, to which they seem most closely affiliated, the digestive tract curves back upon itself and ends near the mouth. The opening of the mantle is sharply restricted at the base of the tentacles, where it forms a single siphon, which serves for ingestion, egestion, and movement. By expelling a jet of water through the siphon, the squid or octopus propels itself rapidly backward, and some squids can even throw themselves out of the water and skim over the surface like flying fish. In some forms, flattened flaps or folds on the end of the body sac serve as fins and are used in swimming. Octopods also pull themselves along the sea bottom by their tentacles, much as on legs. They even use them to build nests of stones, some quite heavy, which they carry with certain tentacles while they push themselves along with the others. The cephalopod body plan has been modified in a great many different ways in different species (Fig. 285).

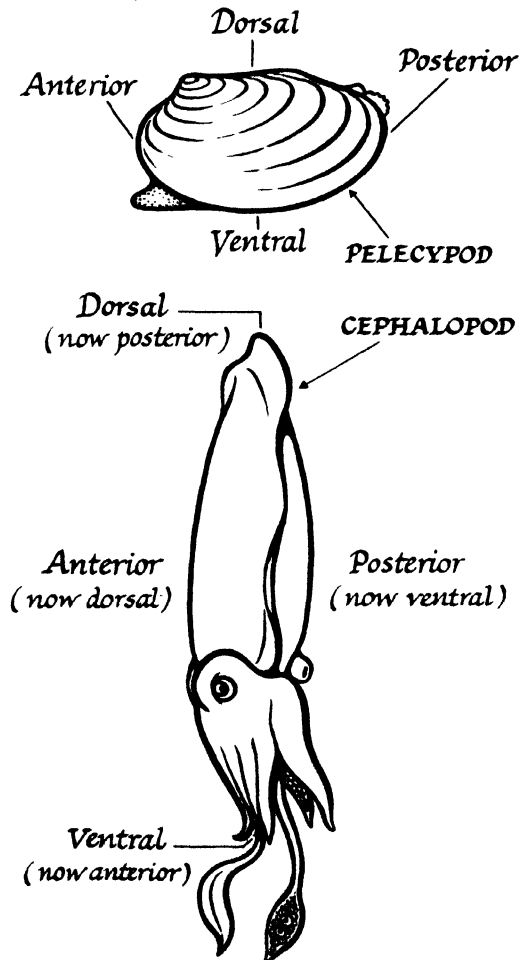
Tentacles. The tentacles are remarkably mobile and of great strength despite their lack of skeletal structure. Armed with double rows of suction cups, the rims of which are sometimes studded with sharp spines or hooks, the tentacles can be firmly attached to almost any kind of surface or object. They thus serve both in locomotion and in drawing prey to the mouth. A parrot-like beak and the rasping radula tear or crush the prey, which is then swallowed piecemeal. Poisons secreted by a specialized salivary gland partially paralyze captured animals. In the squids and cuttlefish, two arms are highly specialized to serve as "lassos" for capturing food. These are

usually carried within the folds at the base of the crown of tentacles but can be hurled out with great speed so that the flap-like end-plates attach themselves to a crab or fish, which is then hauled into the mouth.

An intestinal sac, the ink sac, produces a dark fluid which is discharged through the siphon in a cloud that creates a diversion and allows the creature to escape a pursuer. This is absent in the cephalopod dwellers of the lightless depths of the ocean.

In the cephalopods the blood is circulated wholly in blood vessels rather than partly in blood sinuses. Moreover, the high rate of me-

Fig. 284. Body orientation and axes of a mussel compared with that of a cuttlefish. The cuttlefish is drawn in the same relative position as the mussel. The position is normal for the mussel but not for the cuttlefish, which normally swims mouth foremost.



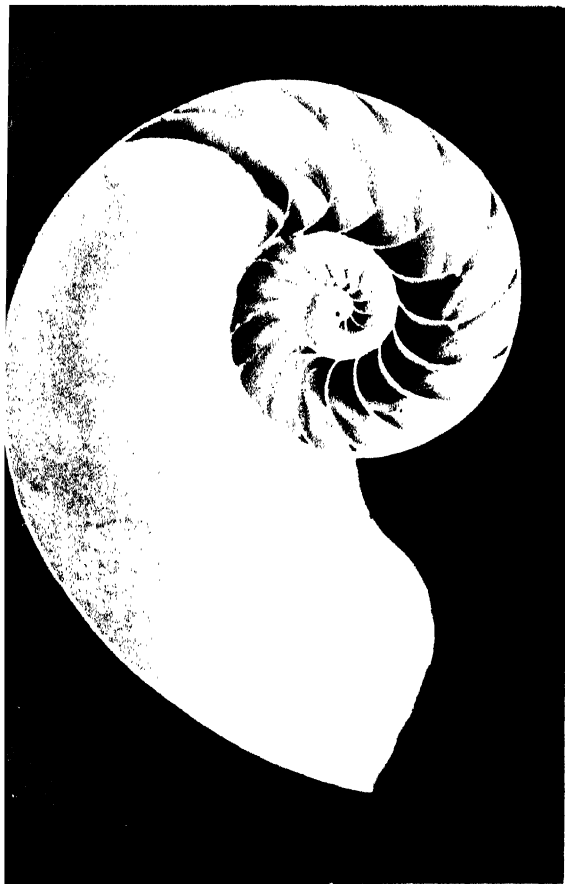


Fig. 285. Shell of the pearly nautilus in section. The shell is coiled dorsally, opposite in direction to the coiling of the gastropods. The nautilus occupies only the outer chamber. Still another type of coiling is shown in the shell of an ammonite of the Cretaceous (right).

tabolism requires efficient respiration, and the gills in the active species are richly filamented. Water is circulated over them by the expansion and contraction of the muscular mantle.

Nervous Development. Every action of a cephalopod bespeaks a nervous development considerably beyond rudimentary coordination. Indeed, we may ascribe to these animals a fair degree of intelligence. Octopods will overcome considerable obstacles in attaining an end, such as a bit of prey, even though much time may elapse between discovery of it and attainment, and despite the fact that it was beyond the immediate reach of the animal's sensory organs. The high coordination, and perhaps even emotion, is also shown by the lightning-like surges of color that flit over the skin of an octopus like flickering northern

lights. These range from red to brown to black, or back to gray and white tempered with iridescence, and are produced by special branched contractile cells in the skin under the control of the nervous system. Pigment granules in these cells may be tightly clustered so that little color shows, spread in a thin dark sheet, or grouped between these extremes. Cephalopods possess olfactory organs, statocysts and tactile organs, but it is their eyes that are most remarkable.

The Cephalopod Eye

The Camera Principle. In its changes of color, as well as in guiding its lively activities, the eyes of the cephalopod play a prominent role. To understand the principle of the eye, we may compare it with a camera, for that is

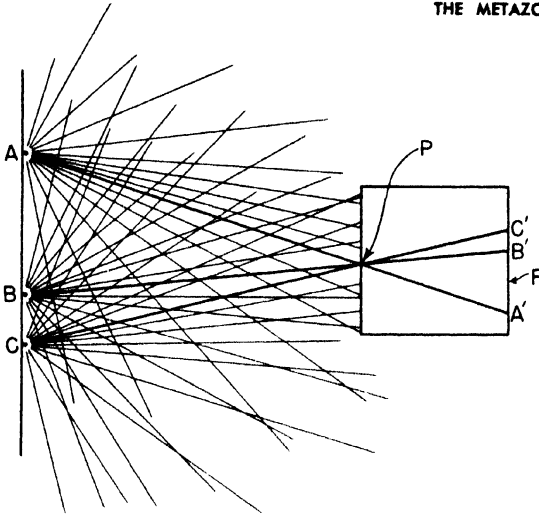


Fig. 286. The principle of image formation with a pin-hole camera. Light scattered from sources A, B, and C may be channeled to a light sensitive surface F by means of a very small aperture or pinhole P.

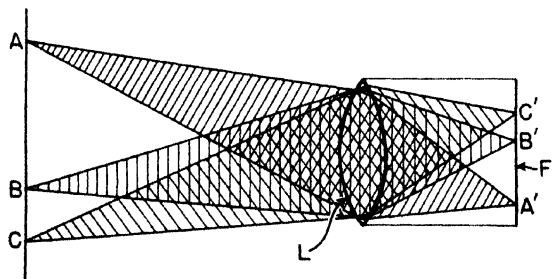
essentially what an eye is. Three elements are essential in any camera (or eye), to which a fourth must be added for real efficiency. These are a light-sensitive surface, an optically insulated box which light enters only through a controlled opening, an image-forming lens, and a device to control the amount of light which enters the box. When light falls on an object, a portion of it is reflected and the balance is absorbed. The reflected light scatters in all directions from each point on the object. A photographic film exposed directly to this scattered light will show no image but will be solid black or gray, since it receives light uniformly. In order to create an image, each "point" of light from the object must be duplicated as a point on the film. This can be done by letting only a thin beam of light from each point reach the film. A small hole in a shield at the front of a camera box will produce this effect; this is the principle of the pin-hole camera (Fig. 286). The image thus produced is inverted, and of course feeble, since only a small part of the light leaving the object reaches the film. Enlarging the aperture increases the amount of light entering but blurs the image, since many beams of light now strike different

parts of the film, and each point of light on the object is duplicated not as a point but a disk.

If a lens is added, it focuses light by bending the rays toward a point in a plane behind the lens and thus prevents a particular ray of light from reaching other areas in the plane. In a glass lens, curvature and thickness determine where the image will fall and how large it will be (Fig. 287). A film in the plane of focus, or convergence, will receive a bright inverted image. If the object now moves closer to the camera, the focal plane will fall behind the film, and the image will lose its sharpness. To bring the image into focus again, either the film must be moved from the lens until it is once more in the focal plane, or a thicker lens must be substituted (Fig. 288).

The Camera Eye. As we have seen, most animals have cells with special light-sensitive structures. These are derived from the skin, and their cells are characterized by free neurofibrillar endings. Neurofibrils, a feature of nerve cells generally, are strands or networks of thread-like fibers within the nerve cell. Wherever light sensitivity occurs, such brush- or thread-like structures are found (Fig. 249). Pigment deposits are usually but not always associated with visual cells, and apparently serve primarily to insulate the cell optically against extraneous light sources. In some organisms, such as the earthworm, light-sensitive cells are scattered over the surface of the animal. In others, as in some snails, they come in clusters, and such clusters are the beginning of the eye.

Fig. 287. Light rays falling upon a denser medium at an angle are bent. If the medium is curved to form a lens (L), all light from any point (A, B, or C) will be bent to converge again at a point behind the lens. Because of the lens, the image will be much brighter than in the pin-hole camera, since many "pencils" of light from each point source create the image points on surface F.



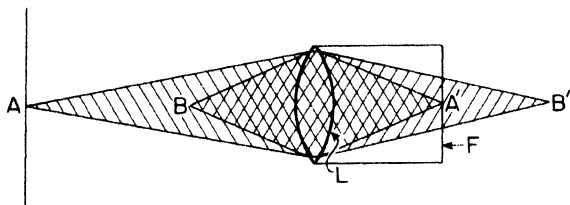


Fig. 288. If object *A* produces image *A'*, object *B* will produce an image behind *F* at *B'*, and *B* is out of focus. By moving *F* far enough from the lens, focus may be reestablished. Or, with a thicker lens, focus could be changed. Thus *A'* could be made to fall in front of *F*, *B'* on *F*. An eye may accommodate for close objects by thickening the lens, a camera by moving the sensitive surface *F*.

To protect these specialized surface areas from mechanical stimulation or injury, many organisms possess pit-like depressions, eye cups, so that the optic layer is sunk beneath the surface. A transparent secreted material may also form a protective layer which fills the cup. Further changes deepen and enlarge the structure, eventually forming a bubble-shaped organ constricted at the outside (Fig. 289). The secretion within the cup acts as a crude lens, focusing all light rays on the light-sensitive surface, which we may now call a retina. Finally, a spherical lens may be differentiated within the secreted mass, and the basic structure of the camera eye is then complete.

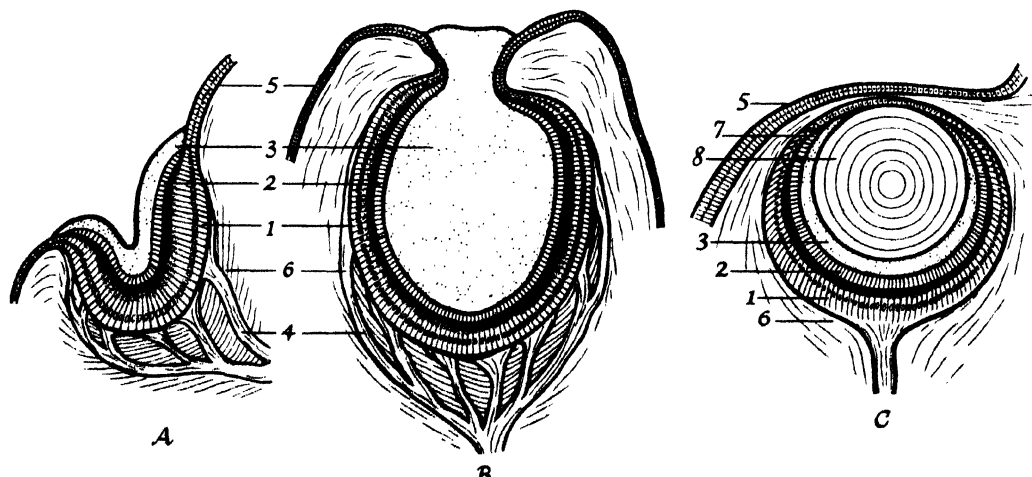
The eyes of the cephalopods are the most

highly developed visual structures among invertebrates, rivaling those in the highest vertebrates (Fig. 290). In size, the eyes of some cephalopods exceed those of any other animal, sometimes reaching a diameter of a foot and a half. In basic structure, they show great resemblance to the vertebrate eye, having the camera-like structure of lens, retina, and optically insulated chamber. But in detail and in development they are quite different, thus indicating their independent origin. Whereas in vertebrates the eye cup, including the retina, arises from an outgrowth of the brain, in the cephalopods these structures all have their origin in the ectoderm. Hence in the cephalopods a separate optic ganglion, located behind the eye, concentrates in it the complex ganglionic connections found in the vertebrate retina. Nevertheless, the cephalopod eye and the vertebrate eye present one of the most striking cases of convergent evolution, in which entirely different original structures and totally different courses of evolution have resulted in organs strikingly similar in design.

Reproduction

Cephalopod reproduction is always sexual, and the individuals are males or females, not hermaphrodites. In some species, males and females are quite different, but as a rule, the sexual differences are minor except in one or more of the tentacles. Thus the shell-less male

Fig. 289. Diagrammatic median section through gastropod eyes. *A. Patella*, a simple snail. *B. Haliotis*, the abalone. *C. Buccinum*, the whelk. 1. Light-sensitive cells. 2. Rods. 3. Secreted mass. 4. Optic nerves. 5. Epidermis. 6. Connective tissue. 7. Anterior wall of optic cup. 8. Lens.



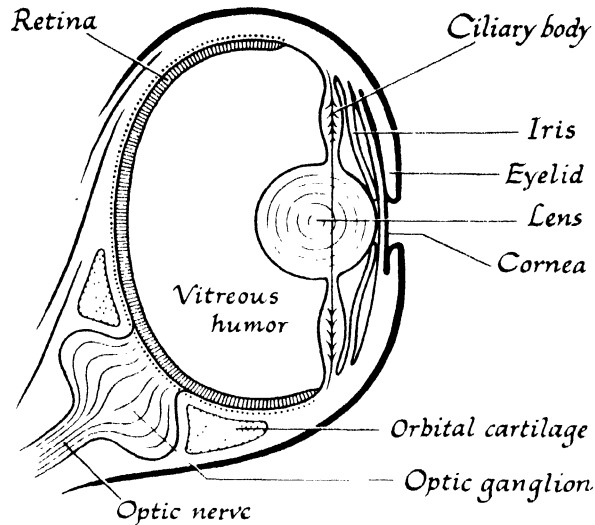


Fig. 290. Cephalopod eye. Eye of squid. Though the elements of this "camera eye" are derived differently than those of the vertebrate eye, the end results are strikingly similar. Unlike the eyes of planaria and of vertebrates, this retina is not inverted.

of the paper-nautilus, *Argonauta argo*, is much smaller than the female, and its third left arm develops in a very different manner from the other seven. In its earlier stages this organ lies rolled up within a special capsule, which bursts to release it when the time for the performance of its function arrives. In mating, this specialized arm is inserted into the mantle cavity of the shelled female, separates from the male, and for some time carries on an active and independent existence within the mantle cavity of the female (Fig. 291). A sperm capsule, carried by the special organ of the male, has within it a special apparatus that swells by absorbing water and explosively scatters the sperm inside the mantle cavity, thus bringing about the fertilization of the eggs. There are similar structures in other cephalopods, but *Argonauta argo* represents perhaps the highest degree of such differentiation. The female nautilus is distinguished by a strikingly beautiful chambered shell, secreted by the two dorsal arms. The shell serves as a cradle for the eggs until they are hatched.

In most species of cephalopods, the eggs are laid either singly or in groups and are left to shift for themselves, though in some, the young are retained within the mantle cavity for some time. Some cephalopods are viviparous, and

retain their eggs until the young are hatched. Cephalopod eggs are unusually well supplied with nutritive yolk. Because of this, the cleavage of the embryo is somewhat different from that of other invertebrates thus far discussed, for the inert mass of food does not participate in the cell divisions of the protoplasm. For this reason cleavage is at first restricted to one end, and the embryo thus develops at that end of the egg, like those of some higher animals, such as birds.

Belonging to a sharply separated phylum which has followed an evolutionary road all its own, the mollusks proclaim that highly complex and efficient organisms, with considerable ability to dominate their environment, can evolve by other paths than ours. While the greatest obstacle to their future evolution may be their limitation to life in the water, that is by no means certain. Surely the forebears of man once held no greater promise.

Summary

The members of the phyla described in this chapter are our contemporaries. They nevertheless illustrate the branching pattern of evolution as well as the wider divergence. As changes accumulate, new tissues develop; organs and

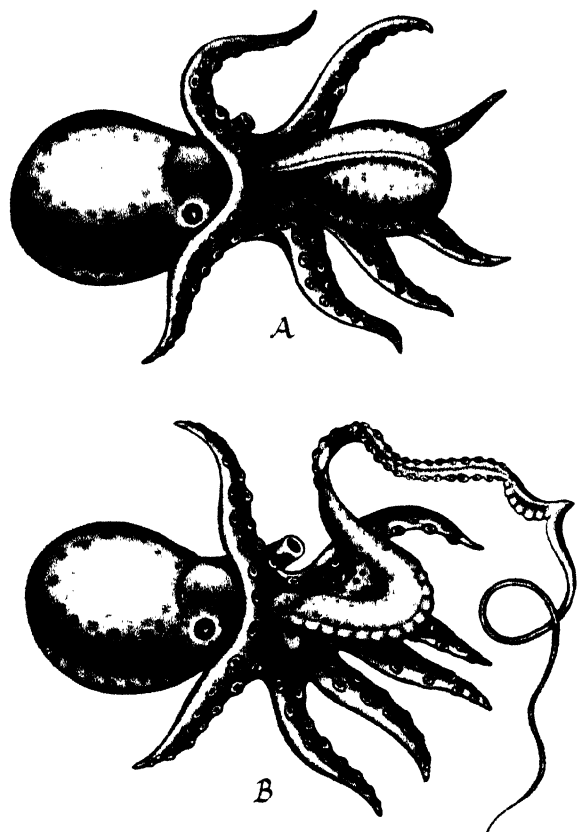


Fig. 291. *Argonauta argo*, male. *A.* The specialized copulatory arm, the *hectocotylus*, still encased in its capsule. *B.* Hectocotylus free and ready to function.

systems of organs are added and refined. The creatures gain increasing sensitivity to their environment and increasing control over it. In some of these phyla, we have seen stagnant conservatism. We have also seen repeated instances of regression and of adaptation to narrow fields of specialization, especially among parasites. But through all this maze of change runs a thread of evolutionary progress.

In the flatworms we saw the first real mesoderm, from which many organ systems were to come, and distinct bilateral symmetry, accompanied by cephalization and a central nervous system. With increased coordination came the beginnings of sense organs, culminating in the eyes of the cephalopods, better coordination in movement, higher metabolism, and the beginnings of an excretory system, seen first in the planarian flame-cells and the rudimentary "kidney" of the lampshells. Along with these developments came tremendous improvements in the digestive system, which in the nemertine worms became an open tube from mouth to anus, and in higher groups evolved such special organs as the pharynx and crop of the earthworm, the stomach, and the digestive gland or liver of the mollusks. Likewise, after the gastro-vascular cavity had given way to an intestinal tract, a circulatory system appeared — at first merely three tubes in the nemertines, but having a rudimentary pumping system in annelids and becoming a real three-chambered heart in the mollusks. As the size of animals increased, a simple respiratory system developed in the form of gills richly filled with capillaries. Gradually sexual reproduction replaced the simpler asexual, regenerative, and budding methods. Males and females succeeded hermaphrodites. Finally, in the annelids, we see for the first time the segmental body structure which is basic to all higher animals except the mollusks. Thus in a sense these phyla epitomize the course of animal evolution. There are set-backs and blind-alleys, "do-nothings" and degenerates, but there is also a clear progression from simple to complex, and from less to more control over the environment.



The Highest Invertebrates: The Arthropods

At some time in the Proterozoic era there appeared an evolutionary pattern which, 500 million years later, was to provide three-quarters of the million or more animal species on earth today and to be as prolific in numbers as in kinds. These are the *Arthropoda* (Gr. *arthron* = joint + *pous* = foot), a phylum which includes centipedes, scorpions, spiders, crabs, shrimps, and the immense variety of insects. The success of the phylum can hardly be overestimated, for arthropods exist in every environment on earth capable of supporting life: on land, in subterranean caverns, in the deepest ocean, in rivers, in salt lakes, in the jungle, in the desert, and in the Antarctic.

Already in that far-off era, the ancestors of the vertebrates and man appear to have taken a different path from that taken by the arthropods. It was probably an annelid-like creature which in that era first evolved segmentation and jointed appendages, characteristics which were elaborated in the trilobites of the Cambrian, and through endless modifications appear to have produced the arthropods of today. Branch after side-branch split off, piling mutation on mutation, often repeating what had evolved independently in other branches.

For reasons rather hard to understand, some of the earliest and simplest modifications have survived, while other forms showing greater refinements have become extinct. On the whole, however, more highly specialized forms have gradually replaced simpler ones, as increased numbers sharpened competition.

General Characteristics

Our frequent contact with insects, spiders, crustaceans, and other arthropods sometimes

dulls our perception of the differences between them and the vertebrates, but those differences are truly enormous. Both groups are segmented animals, and in both the original segments have become so fused and specialized that they have all but disappeared. But the skeleton of the arthropods is outside the body instead of inside, like that of a vertebrate, and for this and other reasons, they are in many ways as rigidly unadaptable as they are highly specialized.

Imprisoned as in a suit of armor, the arthropods cannot grow and develop gradually as vertebrates do, but must molt and undergo a series of quite radical transformations, called *metamorphoses*, growing and changing in spurts from molt to molt, from egg through larva to adult.

Most arthropods, also, have many pairs of jointed appendages, and often these are rigidly specialized to perform certain tasks in a way far beyond anything found among vertebrates. True, horses have running feet, moles have digging feet, and birds have wings. But in the lobster each pair of "legs" is a specialized tool — antennae, jaws, pincers, walking legs, swimmerets — and one kind cannot substitute for another. The bee also carries an impressive set of special tools. But the paw of a raccoon, or the hand of a man, is a comparatively mobile structure which can perform many tasks. Were man built like an arthropod, he would grow his tools — his hammers, saws, and blowtorches — instead of making them, and consequently he would have a limited number.

A similar rigidity pervades the nervous system, and consequently the behavior, of the arthropod. Whereas the highest vertebrates are versatile and highly adaptive creatures, the

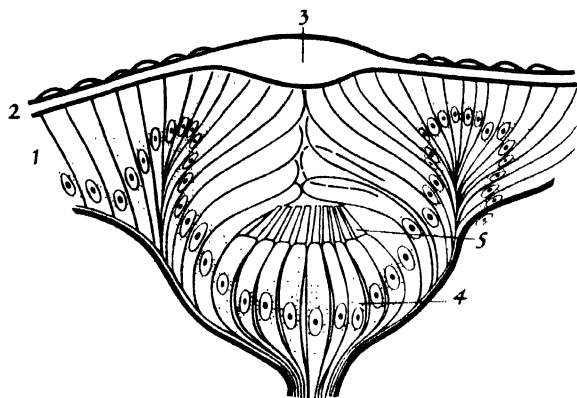


Fig. 292. Median section through the lens-ocellus of a young larva of the water-beetle *Dytiscus*. 1. Epidermis. 2. Cuticular layer. 3. Lens. 4. Visual cells with rods. 5. Nerve processes forming optic nerve

arthropod behaves like an automaton. The story of a predacious wasp, hopelessly entangled in the web of its own instincts, will illustrate. Certain wasps paralyze caterpillars with a sting, then carry them to a sandy spot, dig a hole, haul the caterpillar into it, deposit an egg on the caterpillar, and cover it with sand. It is related that a biologist once placed a second caterpillar on the ground while a wasp was depositing its egg inside the burrow. Having completed the burial, the wasp, confronted by a second inert caterpillar, re-excavated the hole. But finding the first caterpillar, it buried it once more. Then arriving again at the surface and seeing the second caterpillar, the wasp re-dug the hole a second time. In the automatic quality of its response we are somewhat reminded of the broom in *The Sorcerer's Apprentice*. The incident is a striking illustration of the typically rigid pattern of arthropod behavior.

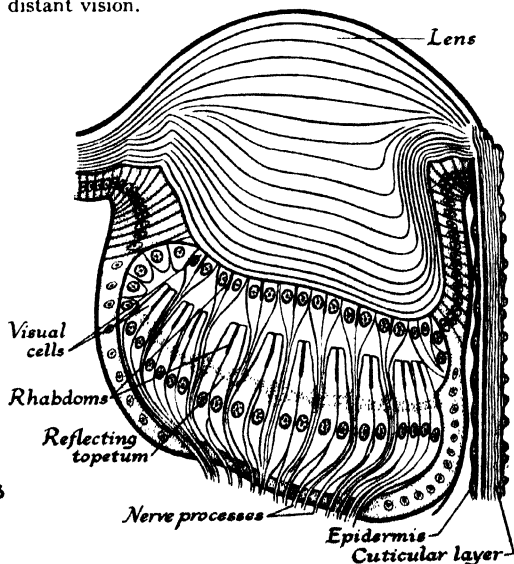
The arthropod and the vertebrate are also quite different organically. Arthropods breathe with leg appendages, with outfoldings of the rectum, or with folds of the skin. Instead of transporting oxygen in a blood fluid, they often pipe it directly through a network of tubes. Although they have a tubular digestive tract divided into a number of specialized organs, these organs only remotely resemble ours and need bear no structural or functional relation to them. They may chew with their "stomachs" or with their

"legs," and they may digest with their "livers." Their "kidneys" or excretory organs may be in the head and open to the outside near the mouth, while the "uterus" may be in the legs. The heart, when they have one, lies in the mid-dorsal region of the body, surrounded by vastly swollen veins which have completely obliterated the true coelom, and form a *hemocoel*. The blood, instead of being red like ours, is pale blue and colored with hemocyanin instead of hemoglobin, due to the presence of copper ions instead of iron; and the hemocyanin is dissolved in the blood plasma instead of being carried in special blood cells, like hemoglobin. Arthropods may have "ears" in their legs, or in the abdomen, they may vocalize with their wings and copulate with their legs. The list of differences is extensive and by no means limited to gross structures.

The Arthropod Eye

One of the most striking general arthropod characteristics, and one of the most remarkable developments in the phylum, is that of the eyes. These are of two kinds, simple eyes, called *ocelli*, and compound eyes, made up of a number of such units. Many arthropods have both types.

Fig. 293. Ocellus of a damselfly (*Agrion*) showing retinal cells arranged in two planes, thus forming an eye with two fixed focal planes, one for near and one for distant vision.



Lenses which serve as image-forming optical insulators are found in many organisms, but they are not all produced in the same manner or from the same tissues. Thus we infer the separate evolution of eyes in different phyla and classes. In insects the lens is created by a thickening of the cuticle above the cup-like ocellus, as shown in the eye of the larva of the aquatic beetle *Dytiscus* (Fig. 292). In certain annelids, the lens is simply secreted material.

Simple eyes form images, but these can be only as clear as the quality of the lens and the number of visual cells in a given area of the retina will allow. Similarly, the clarity of newspaper pictures is sharply limited by the coarseness of the screen used in the reproduction process. The vertebrate eye may have a half million sensitive cells in a single square millimeter of retina — and that is just about the maximum, because of the size of the cells. Only an increase in the size of the eye could further increase definition. No arthropod eye achieves such acuity.

Accommodation in the Simple Eye. The simple eye has a fixed focus (Fig. 293) and produces a sharp image only if the object viewed is at a certain fixed distance. The plane of sharp focus changes only slightly for an object-distance from infinity to a certain minimum distance, depending on the size of the eye. But at any distance below this minimum, the clarity of image is markedly reduced. As we have seen, a camera or an eye can be accommodated to different object-distances either by changing the distance between lens and retina, or by changing the shape of the lens. Cephalopods and, among vertebrates, the fishes have evolved eyes that accommodate by moving the lens forward or back, as in a camera. Birds and mammals have an elastic lens which changes in shape.

But in some arthropods the lack of accommodation within the eye has been remedied in quite another way: there are different sets of eyes, with different fixed foci, some for near and some for distant vision, a little like bifocal glasses. The ocelli of spiders (arachnoids) are like this. The dragonfly combines two ocelli of

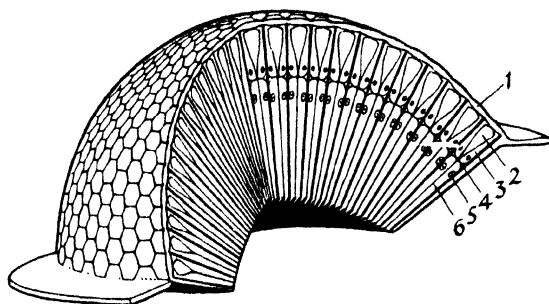


Fig. 294. The compound eye of the insect, in section. 1. Corneal lens. 2. Crystalline core. 3. Pigment and corneagenous cells. 4. Lateral pigment cells. 5. Nucleus of visual cell. 6. Rhabdom or rod.

different focal length into one eye, with a retinal layer close to the lens for distant vision and another, farther away, for near vision (Fig. 293). Just how such vision registers on the brain of the animal we cannot say, but a certain perspective or depth of image is probably obtained.

The Compound Eye. A highly complex eye has relegated the simple ocellus to second place in most arthropods. This is the great compound eye so familiar in insects, one on each side of the head. The compound eye may be traced to a type of light receptor found in annelids, with epithelial visual cells surrounded by pigmented tubes. In some annelids these are scattered over the gills with the openings of the tubes aimed out fanwise over a comparatively wide field of vision. In others, these tubular ocelli are arranged in groups or clusters, and in still others they are so closely crowded as to leave almost no space between them. The cluster in fact becomes a compound eye, the organ which reaches its highest perfection in insects (Fig. 294). The individual unit of a compound eye is called an *ommatidium* (Gr. dim. *omma* + *atos* = eye), and is homologous to a single ocellus. It consists of a corneal lens, a crystalline cone, pigment- and cornea-producing cells, lateral pigment cells, and a light-receptive rod.

Vision in the Compound Eye. Since the light-receiving structures in an individual ommatidium are a single fused unit, they do not form an image as in an ocellus, which has a retina

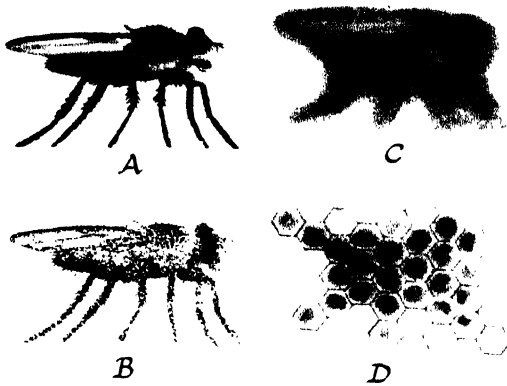


Fig. 295. Image formation in man as compared to that in the dragonfly. *A.* The image as the human brain "sees" it. *B.* Actually the human retina registers only as much of the image as actuates the rods and cones; hence the retinal image is a fine mosaic. *C.* The crude irregular mass is probably about what the dragonfly sees when it looks at a fly, since the individual image is probably a fused mass. *D.* A section of a dragonfly eye with the image of the fly superimposed to show which ommatidia are affected.

of many separate light-receptive units. Each ommatidium can register only light or darkness, and each records that portion of the object upon which it is trained. The sum of these impressions must produce a mosaic picture of the object. This sort of vision is called "mosaic vision" (Fig. 295). Generally the light entering an ommatidium is limited to the rod by the insulating layers of lining pigment, and only light that falls almost vertically into the structure reaches the rod. Since all other light is absorbed by pigment layers, the efficiency of such an eye is quite low. In certain nocturnal insects, the peripheral layer of pigment may be lacking or movable. This of course greatly increases the sensitivity of the eye and more than offsets the lowered acuity of vision. Although

compound eyes are quite rigid structures, they accommodate for different distances of the object by a mechanism similar to that in simple ocelli. In one part of a compound eye the axes of the ommatidia may diverge only slightly and in another part quite sharply; or there may actually be two eyes, one adapted to near and one to distant vision.

MINOR ARTHROPODS

The Trilobites

If we include the extinct trilobites (see pages 101-102), we may say that there are seven classes of arthropods, showing varying degrees of specialization, from fairly simple legged "worms" in which the segments are more or less alike, to the most highly developed crustaceans and insects, in which the segments are often fused almost beyond recognition. The trilobites were aquatic creatures probably allied to the crustaceans — they had shells, jointed legs, and antennae, and a body which foreshadowed the division into head, thorax, and abdomen characteristic of insects and many other arthropods.

Peripatus

Perhaps the most primitive living arthropod is *Peripatus*, the only member of the small class *Onychophora* (Gr. *onychos* = claw + *pherein* = to bear) — although this group is sometimes considered a separate phylum intermediate between annelids and arthropods (Fig. 296). Though not an actual link, the creature is of a type that could have been transitional between these two groups, for at first glance it shows definite characteristics of both and seems merely to have stopped midway in its career. In a way this is true, but it is probably more accurate to say that *Peripatus* ran a more or less parallel

Fig. 296. *Peripatus*, a "link," shows characteristics of both annelids and arthropods.

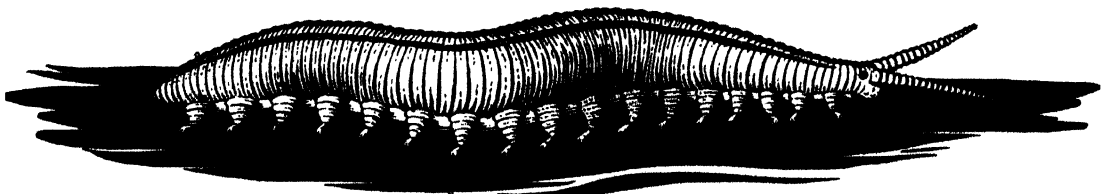




Fig. 297. The centipedes (left) and the millipedes (right) are interesting intermediates between *Peripatus* and such highly specialized arthropods as crustaceans and insects.

course with other creatures that evolved from annelids to higher arthropods and merely stopped developing sooner.

Peripatus looks somewhat like a caterpillar with a pair of antennae, and a thin, slightly accordion-pleated skin covered with small warts. Externally it gives little evidence of metamerism except for its segmental legs. These are not jointed like those of typical arthropods but are fleshy bumps armed with sharp claws. Only its first three segments are fused into a head and mouth parts, in contrast with the usual six or seven of most arthropods. But fusion to any degree approaches the arthropod plan.

The muscular structure of *Peripatus* is somewhat like that of annelids, being made up of continuous longitudinal and circular layers rather than arranged in bundles, as in other arthropods. The tubular digestive tract is simple. In its early embryonic life, *Peripatus* has a circulatory system similar to that of annelids, with veins, arteries, and a true coelom. As it develops, the veins enlarge and gradually squeeze the coelom out of existence, creating the large hemocoel characteristic of the arthropods. Oddly, the arthropod-like respiratory system of tracheal tubes was probably evolved independently by *Peripatus*. The excretory system consists of segmental coiled structures similar to the nephridia of the annelids. These are equipped with cilia, which are notably absent in other arthropods. There is a double nerve cord with ganglia, again similar to the annelids. Also as in the annelids, the reproduc-

tive structures are ciliated. Fertilization, however, is internal, and there is no larval stage — clearly such an adaptation to land life as that of the earthworm and of no phyletic significance. The fact that this animal has been variously called an annelid, an arthropod, and a member of a separate phylum is excellent evidence for evolution. It is clearly an intermediate.

Centipedes and Millipedes

Two other fairly primitive arthropod groups are the centipedes, class *Chilopoda* (Gr. *cheilos* = lip + *pous* = foot), and the millipedes, class *Diplopoda* (Gr. *diploos* = double). Both have mainly uniform segments as does *Peripatus*, though the head consists of four fused segments instead of three, and three other segments bear chewing appendages which are derived from modifications of the foot, as are the antennae also. The voracious and predatory centipedes have powerful mandibles, incurved hooks large at the base to accommodate poison glands and perforated at the tip for the exit of the poison duct (Fig. 297). The millipedes, however, are peaceful vegetarians with weak mandibles and no poison glands. They live in moist places under stones and logs and eat decomposing vegetable matter.

The serpentine body of the centipedes is composed of flattened segments, each with one pair of long, jointed legs. In the millipedes, however, the body is cylindrical, and each segment in the adult is literally double, as the scientific

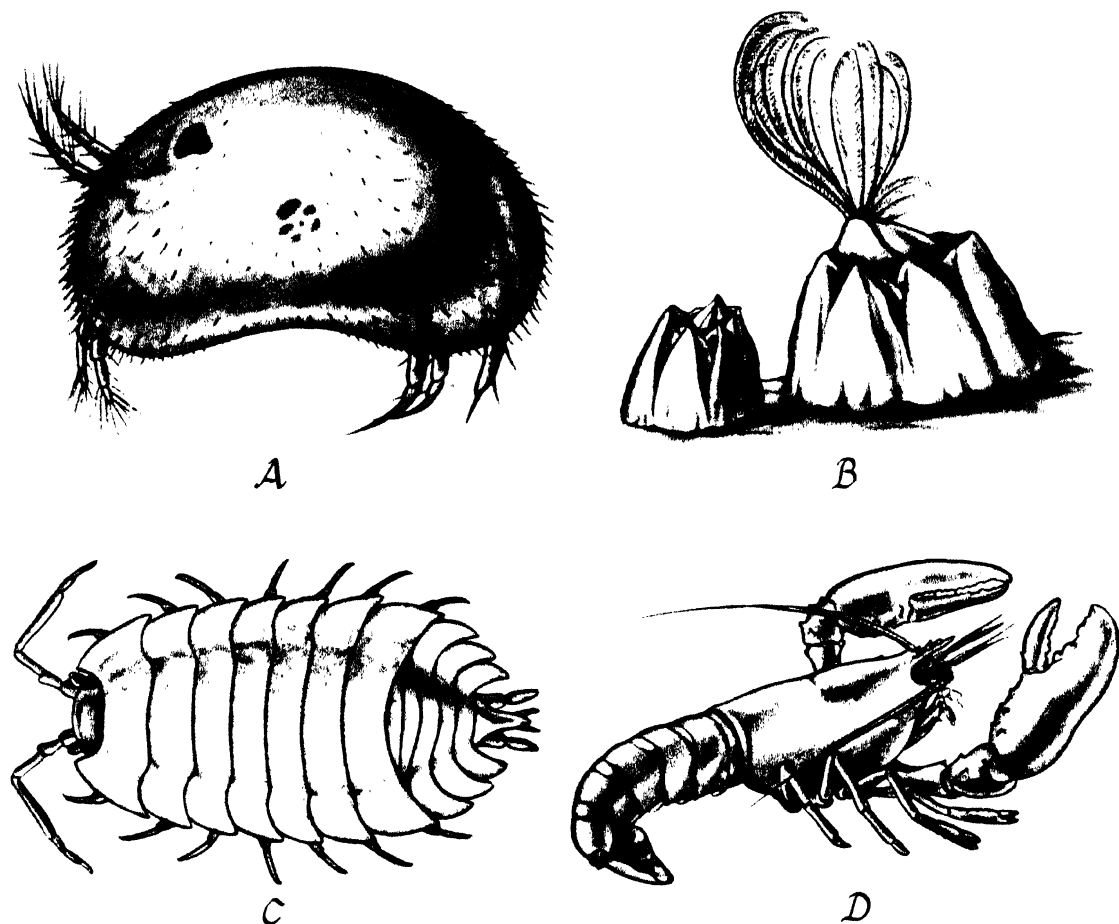


Fig. 298. Representative crustaceans. *A. Cypris*, an ostracod. *B. Balanus*, the acorn or rock barnacle. *C. Oniscus asellus* — the sow-bug — an isopod. *D. Homarus*, the lobster — a decapod.

name of the class implies, for it is a fusion of two embryonic segments and bears two pairs of legs. Large centipedes are as much as twelve inches long, and their bite has been fatal to human beings. In the centipedes the reproductive system has a posterior opening, but in the millipedes it opens quite far to the front, in the third segment. In spite of their differences, the two groups clearly represent stages somewhere between the generally uniform segmentation of the annelids and the high specialization of segments found in the higher arthropods. For the fused segments of the head, and their specialized appendages, are much like those of many insects, and there are jointed legs; but the body segments are still all much the same. Both

groups, however, are fairly small in numbers of species.

THE CRUSTACEA

Not so the crustaceans. While they are surpassed both in numbers and variety by the insects, the members of the class *Crustacea* (L. *crusta* = crust) are a large and diverse group, ranging in size and shape from the tiny water fleas, fish lice, and barnacles — some microscopic crustaceans are less than a millimeter in length — to the lobsters and giant crabs with a foot spread of ten feet or more (Figs. 298 and 302). The waters of the world, both fresh and salt, teem with billions of crustaceans, and a few have even become established on land.

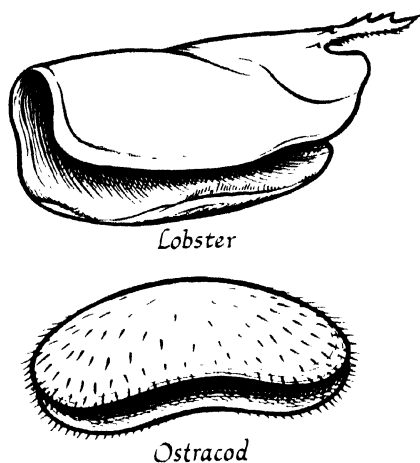


Fig. 299. Two forms of body protection grown by crustaceans, the single median carapace of the lobster, and the bilateral bivalve shell of the ostracods, which is quite minute.

The class is estimated to contain about twenty-five thousand species, as compared to fully seven hundred and fifty thousand species of insects. And the crustaceans show a full range of evolutionary variation from primitive creatures almost like trilobites in uniformity of segments to the highly differentiated crabs and crayfish. Most crustaceans are free-living, but some have become parasites, like *Sacculina* (page 113).

General Characteristics

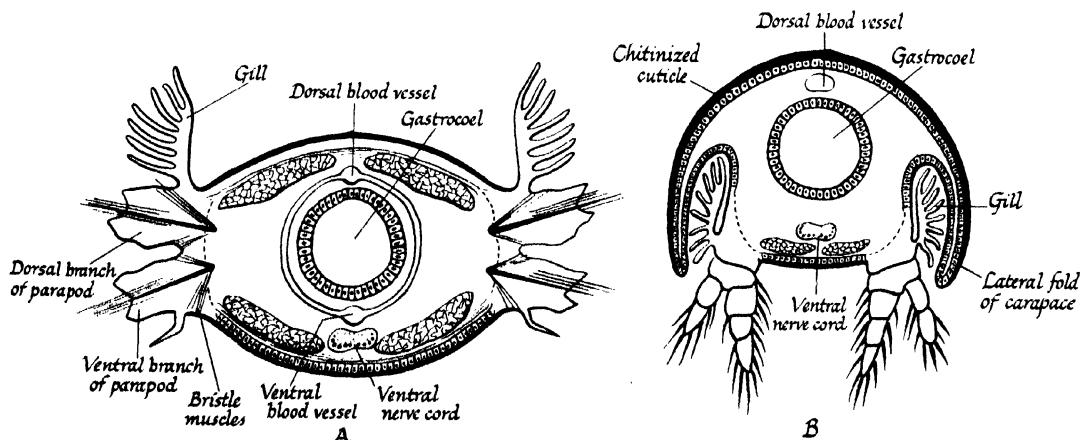
Body. Crustaceans have a chitinous exoskeleton, often stiffened with lime deposits. The

body is usually divided into *head*, *thorax*, and *abdomen*, although in higher forms the first two fuse to become a *cephalothorax*. A skin fold grows back from the head and produces in some species a stiffened cape-like exoskeletal structure, the *carapace*, as in the lobster. In others the fold assumes the form of two shield-like structures, left and right, which enclose the entire animal, including the head (Fig. 299), somewhat like the shells of a clam.

Gills. Most crustaceans have gills, which in many higher forms are enclosed in the carapace and are thus kept moist, making temporary land-life possible. Real land forms, such as the wood-lice or sow-bugs, have branched respiratory tubes, or tracheae, similar to those of the insects and *Peripatus*, but apparently evolved independently. Since gills must be located where ample circulation of water is possible, it is not surprising that moving appendages may be partially or entirely transformed into gills. Smaller forms often have no gills and their respiration is simply by diffusion through the body surface.

Appendages. The characteristic appendage of the crustacean, found in no other arthropod, is *biramous*, or forked, and consists of two segments, to which are attached forked branches: the outer one a potential swimming arm, and the inner one a potential walking arm (Fig. 76, page 111). In swimming forms the whole appendage, but especially the outer fork, may become a paddle or oar. In walking forms the outer fork disappears entirely, and the inner

Fig. 300. Diagrammatic cross-sections of polychaete annelid, A, and crustacean, B.



one, now merely a continuation of the two basal segments, becomes a jointed walking leg. In some crustaceans, secondary appendages support the gills. In cross-section, a "typical" crustacean is interestingly similar to a polychaete annelid (Fig. 300), and it would be difficult to miss the phylogenetic implications of such a fact. Move the feet of the annelid down on its body, increase their size and joint them, pull a skin fold from the back over the gills, blow up most of the veins, modify the muscular system — and the annelid becomes a fair example of a primitive crustacean.

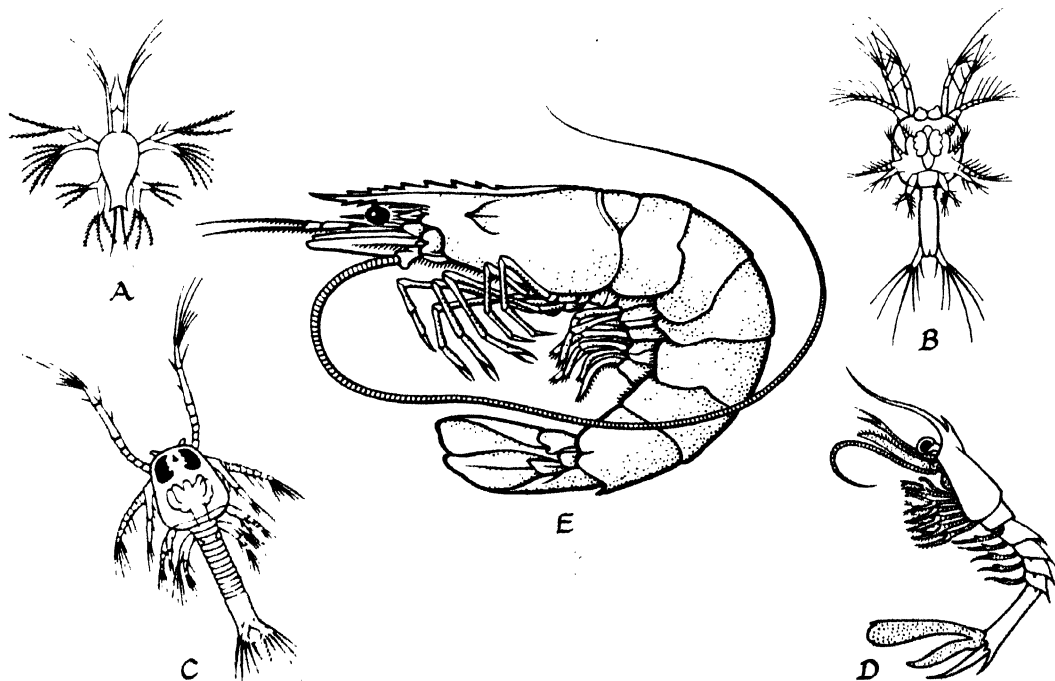
The appendages of the abdomen generally retain their primitive characteristics. Even those of the head, though highly modified as jaws and other feeding organs, show their original forked nature (Fig. 301). Even the walking legs of the lobster, which have quite lost the outer fork, show their biramous origin in the larval stages.

In some crustaceans the second pair of appendages may lose their sensory function and become powerful oars, as in the nauplius type of larva (Fig. 78, page 113) and the freshwater copepod, *Cyclops*.

Internal Organs. The digestive tract varies considerably among crustaceans. It often begins with a chewing organ, back of which is the "liver" — really an elaboration of the intestine and not to be compared to the vertebrate liver. The heart may be tubular or sac-shaped, and may or may not have arteries. In some small species it may be entirely lacking. The kidneys, often called the "green glands," are long coiled tubes that lie in the head region and open to the outside near the mouth. In embryonic stages, their segmental arrangement suggests a homologous relationship with the annelid nephridia, the excretory organ.

Sense Organs. Crustacea frequently have both a simple median eye and a pair of compound eyes. There are also organs of touch and of a chemical sense something like taste. These are hairs or bristles projecting through tiny openings in the shell. About a hundred thousand of them are said to be distributed over the pincers and walking legs of a lobster. Finally, the higher crustacean may have *statocysts* or organs of equilibrium. A statocyst is a capsule located in the base of the antennule, or first antenna, opening by a pore to the outside. On

Fig. 301. Stages in the life history of a shrimp. A. Nauplius. B. Protozoa. C. Zoea. D. Mysis. E. Adult shrimp.



the floor of the statocyst is a band of sensory hairs connected with nerves. The crustacean inserts fine grains of sand into the statocyst after each molt of the exoskeleton. As the animal's position changes, different sensory hairs are stimulated by the tumbling sand grains, and so the creature orients itself with respect to gravity.

Reproduction. Reproduction in crustaceans is sexual, and the sexes are separate except in some sedentary and parasitic forms. Fertilization is generally internal, and the usually unflagellated sperm is often transferred to the sexual opening of the female by a tube-like structure. In many species the developing eggs are attached after being fertilized to the swimmerets on the underside of the abdomen of the female. Some small crustaceans are *parthenogenetic*, that is, their eggs mature without being fertilized, and in some species males are practically unknown.

Crustaceans usually have a complex metamorphosis, one often involving three distinct larval stages, though in some species this has disappeared under the selective demands of the environment. For types that live in rapid streams, for instance, a prolonged independent larval period would cause the loss of most of the larvae downstream. Hence in such species the free-living larval period is generally brief or absent. Moreover, there is a close relation between the size of the egg and the length of the larval period after the young are hatched. In *Penaeus*, a form which has a complete series of larval stages, the egg is very small — $\frac{1}{4}$ mm. in diameter. In the lobster, with a larger egg, measuring 1.9 mm. in diameter, the nauplius or first larval stage is skipped. And in the crayfish, in which the egg is quite large (3 mm.), there is no free-living larval stage and the young never grow biramous appendages on the thorax.

TYPES OF CRUSTACEANS

Of the five subclasses of crustaceans, the most primitive is the *Copepoda* (Gr. *kope* = oar), whose representatives have sixteen uniform segments (head, six; thorax, five; abdo-



Fig. 302. A branchiopod crustacean, *Daphnia* the water flea.

men, five). The thorax bears a pair of typical biramous or forked appendages on each segment, and often those of the head show their forked origin. There are no gills, the heart is small or absent, and the "liver" is regularly absent. The digestive tract is remarkably simple. Reproduction is sexual, with sexes separate, and there is a nauplius larva. Copepods swim with a flea-like motion, aided by greatly enlarged antennules like oars. Fresh-water types, like *Cyclops*, can be found in any pool or puddle.

Somewhat more highly specialized are the members of the *Branchiopoda* (Gr. *branchia* = gills), small fresh-water crustaceans showing a remarkably continuous series of developments. Some forms, like the fairy shrimp, *Branchipus* have on the thorax many segments and forked appendages modified for respiration. Some, like *Branchipus*, have no shield; others have a single dorsal shield, and still others double valve-like shields, like *Daphnia pulex*, the water flea (Fig. 302). In the simpler forms, the appendages are leaf-like. In higher ones, the antennae have become large oars, while the remaining appendages are simple legs. The characteristic branchiopod appendage, in contrast with that of a copepod, has a small everted gill-sac at its base and leaf-like forked end segments. The simple eye of the copepod has in the branchiopod been augmented by a pair of compound eyes, and the digestive tract possesses the characteristic crustacean liver.



Fig. 303. The crayfish, one of the Malacostraca.

There is also a simple tubular or sac-like heart.

Reproduction is complicated by the changing conditions in fresh water. Parthenogenesis is common, though "winter eggs" require fertilization and fertilized eggs may also be produced in summer under favorable feeding conditions. Such eggs frequently require either freezing or drying before they undergo cleavage. *Artemia*, the brine shrimp, can live in the saltiest waters. It is about the only animal denizen of the Great Salt Lake in Utah. Branchiopods, like copepods, are vitally important as food for larger aquatic animals.

Another fairly simple group is the *Ostracoda* (Gr. *ostrakon* = tile, shell), made up of minute shelled animals which look like miniature clams and may attach themselves to algal growth on the glass walls of aquaria. Abruptly, the shells gape a bit, tiny filament-like appendages appear, and the animal darts rapidly through the water (Fig. 298). Both pairs of antennae serve for locomotion, and are sharply curved downward and equipped with bristles. A forked tail serves as a pusher. Anterior appendages are differentiated into specialized mouth parts. Generally with separate sexes, some are parthenogenetic.

Still another minor group is the subclass *Cirripedia* (L. *cirrus* = curl, ringlet). These are the barnacles, commonly seen at the seacoast on exposed rocks at low tide when their white,

crater-like shells are closed (Fig. 298). With the return of the tide, the shells open and the barnacle extends a claw of incurved, finely feathered, biramous appendages that incessantly beckon like crooked fingers, seeking for food. They differ from other crustaceans, except the parasitic ones, in having abandoned locomotion except in the nauplius stage of life. In adaptation to their sedentary life, they are hermaphroditic.

Barnacles cling to any solid object, though some are so specialized that they attach only to specific larger organisms, such as whales. Some have thus become parasitic. The highly adapted and interesting *Sacculina* has been assigned to this group. Interesting historically is *Lepas anatifera*, commonly, the goose-barnacle. The term "anatifera" refers to the production of ducks or geese, and comes from the time when barnacles were thought to grow on trees, fall into the water, and there develop into geese. Thus geese became "fish," and this bit of nature lore helped to relieve the monotony of the fast periods.

Finally, the most familiar group of crustaceans is the *Malacostraca* (Gr. *malakos* = soft + *ostrakon* = shell). This group includes the orders *Amphipoda*, *Isopoda*, and the important *Decapoda* — the shrimps, crabs, lobsters, and crayfishes. The amphipods are uniformly segmented and aquatic, with thoracic appendages developed as walking legs and with characteristic biramous abdominal appendages. The leaping, snapping beach-flea belongs to this group. The isopods include the terrestrial wood-louse or sow-bug (Fig. 298), which has independently acquired tracheae similar to those of the insects.

The decapods, by far the largest group among the crustaceans, are characterized by the fusion of the first thirteen segments into a cephalothorax, of which eight form the thorax. The first three thoracic appendages have usually become mouth parts, thus leaving five pairs of walking legs, from which the order derives its name. These are not forked after the larval stage, but the mouth parts and the abdominal appendages remain so. Pincers or claws are

frequently formed by a projection growing from the next to the terminal segment so that the last two segments oppose one another like a pair of pliers. In complexity and specialization, there is an immense distance between the simplest copepods and such creatures as crayfish and lobster.

THE CRAYFISH

Cambarus, the common crayfish, is a fairly representative decapod. This freshwater miniature of the lobster may be found in ponds and streams, hiding in rocky pools, usually actively scavenging a living of organic debris. Restlessly waving antennae and reasonably effective eyes mounted on movable stalks make it difficult to approach the animal unobserved. Constantly active mouth parts, the *maxillipeds*, perform peculiar shoveling or paddling motions and give the otherwise immobile crustacean features interesting facial expressions. The large first pair of walking legs has been transformed into two effective pincers used mainly in defense. Small and delicate claws on the following two pairs of walking legs are used with surprising skill to pick up stray bits of food, which are then daintily passed forward to the mouth. Much of this feeding is performed underneath the body, out of sight, and thus blindly. But the groping, tapping motions of these feeding claws are far from "blind" chem-

ically and tactually, for claws and legs are covered with innumerable bristles which are sense organs. Small fragments of food strewn over the floor of the animal's container will be selected with unerring accuracy from fragments of inedible material. Through the constant motion of its mouth parts and the periodic flapping of its abdominal appendages, the animal maintains a circulation of water over the gills, which are hidden by the ventral edges of the carapace. Because the gills are enclosed, a crayfish is about as well adapted to land life as a frog is to life in the water. In some regions crayfishes regularly visit river-bank gardens for their food, retreating to burrows with moundlike openings which lead down to the water level.

The abdomen of the crayfish is almost a solid mass of muscle, which can snap the tail parts down and forward with surprising force, propelling the animal backwards with a sudden burst of speed. But this usually happens only in emergencies, and the crayfish usually crawls slowly forward.

The Appendages

Like those of decapods generally, the appendages of the crayfish are highly specialized (Fig. 304). The antennule and antenna not only serve for touch and taste, but the former contains the statocyst and at the base of the

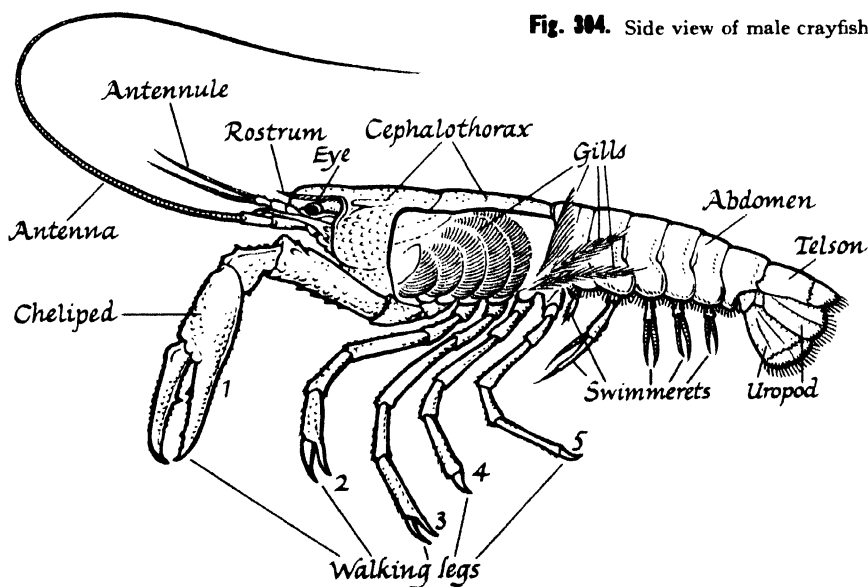


Fig. 304. Side view of male crayfish.

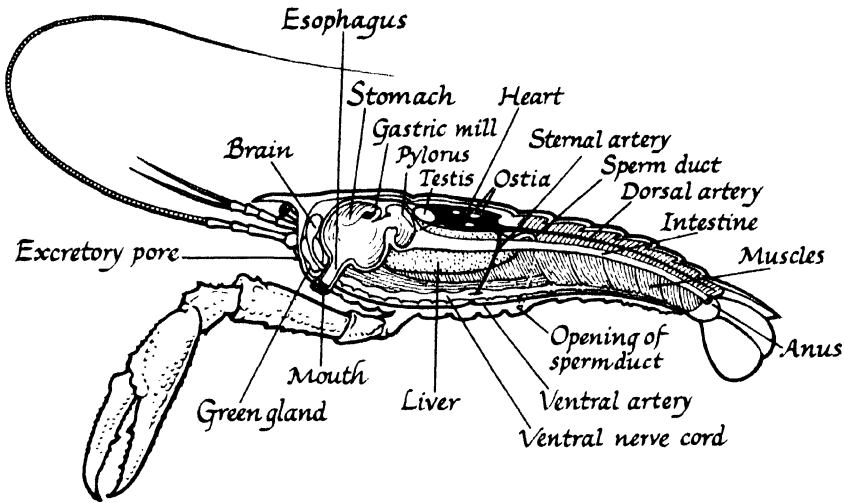
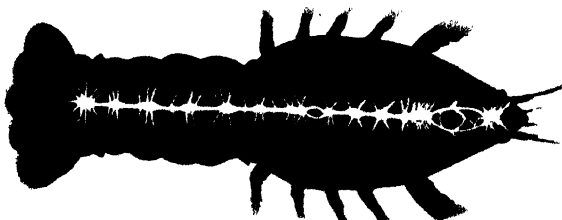


Fig. 305. Longitudinal section of the crayfish showing position of primary internal organs.

latter is the excretory pore. The third appendage, the mandible, is a crushing jaw. The two next, the maxillae, handle food and help circulate water over the feathery gills, of which there are seventeen on each side, attached to the body wall and the bases of the walking legs (Fig. 304). The three maxillipeds follow. Of the five pairs of walking legs, the first pair have fighting pincers and the next two pairs of feeding pincers. Of the six pairs of abdominal appendages, all are swimmerets except the first two in the male, which are tubular copulatory organs, and the first of the female, which is reduced to a vestigial condition. The swimmerets produce water currents and serve as a place of attachment for eggs and young. The last pair of appendages is broad and flat, and its biramous parts supply the two lateral flaps of the powerful tail to each side of the midpiece. (See also page 111, Fig. 76.)

Fig. 306. Nervous system of crayfish.



Organ Systems

The digestive tract also is rather highly specialized. Food passes into the cardiac portion of the stomach, a storage chamber, behind which are three tooth-like structures making a gastric mill, which grinds coarse particles into bits. When ground fine enough, the food passes through a strainer composed of bristles into the second part of the stomach. Here the ducts from the digestive gland, or liver, open. After digestion, the food goes to the uncoiled intestine, where it is absorbed.

The circulatory system is "open," in contrast to the closed ones in the phyla hitherto discussed. Blood is pumped by the heart through the arteries and out the open ends of capillaries into large scattered sinuses. From there it goes through channels to the gills, and after picking up fresh oxygen, returns to a space surrounding the box-shaped heart, which it once more enters through slit-like openings with valves (see Fig. 305). If we imagine the veins of an earthworm greatly enlarged until they more or less fill the coelom, we have a system similar to that in the crayfish. It appears to be quite an efficient system, since it supports an active metabolism.

There are two excretory organs, the green glands, which are anterior to the mouth and

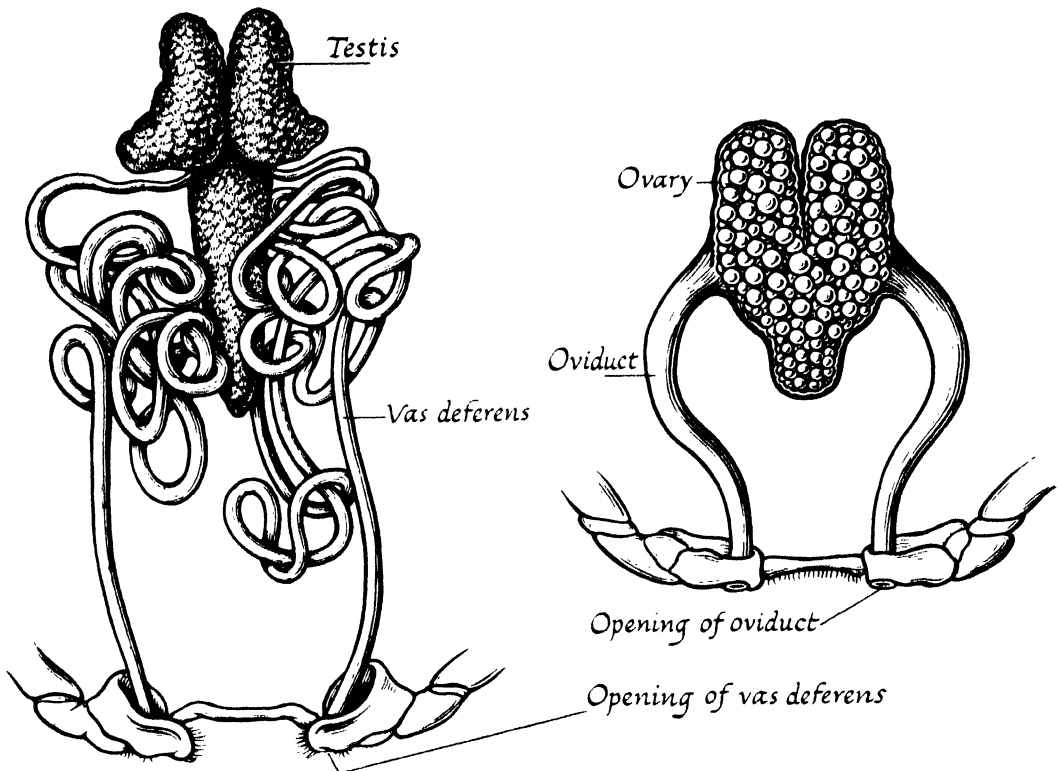


Fig. 307. Reproductive system of male (left) and female crayfish.

open to the outside through a pore at the base of the antenna. These organs, consisting of a green glandular portion and a sac-like bladder, remove wastes from the blood.

The central nervous system of the crayfish is basically similar to that of the earthworm (Fig. 306). A double ventral chain of ganglia ends in a large ganglion beneath the esophagus, around which passes a ring to connect to the main dorsal ganglion, or brain, in the head. The efficiency of the eyes is enhanced by their movable stalks, which help to compensate for the lateral fusion of the body and its relative clumsiness.

In reproductive structures also the crayfish is fairly representative of other decapods. In both sexes the gonads lie just ventral to the heart. In the female a pair of oviducts leads from the ovaries to the base of the third walking legs, and in the male coiled sperm ducts lead to the bases of the fifth walking legs (Fig. 307). In copulation the sperm is transferred to a seminal receptacle, a depression on the

ventral surface of the female, and remains here from fall until the eggs are laid the following spring. As the eggs are laid, they pass over the openings of the seminal receptacle and are fertilized by the stored sperm. They are then passed by the appendages back to the swimmerets, where they adhere until hatched. A slender thread attaches each young crayfish to its egg shell and tethers it to its mother until after its second molt. Life in fresh water, and especially in flowing streams, appears to have selected against an independent larval stage, probably because small larvae would be swept downstream.

Regenerative Power

Although incapable of asexual reproduction or budding, the crayfish still retains remarkable powers of regeneration. A leg or a claw caught too tightly is automatically severed from the body and discarded with apparent unconcern. After a few molts it is replaced with a new member. At times the regenerative process



Fig. 308. A scorpion. Note the sting at the end of the tail.

appears to go astray, so that an antenna may replace a lost eye — a fact which may suggest a relationship between the two.

While perhaps the crayfishes and their close relatives — the crabs, shrimps, and lobsters — are mainly important to mankind as food, they are also of great interest as the highest of the crustaceans — creatures in which the original segmentation is often obscured and overlaid, and in which the original jointed leg has become highly and delicately specialized to perform a great variety of tasks. But while these creatures, and the crustaceans generally, are a diverse and successful group, they are far surpassed in these respects by the highest of the arthropods, the arachnoids and the immense class of the insects.

THE ARACHNIDS: SPIDERS AND THEIR KIN

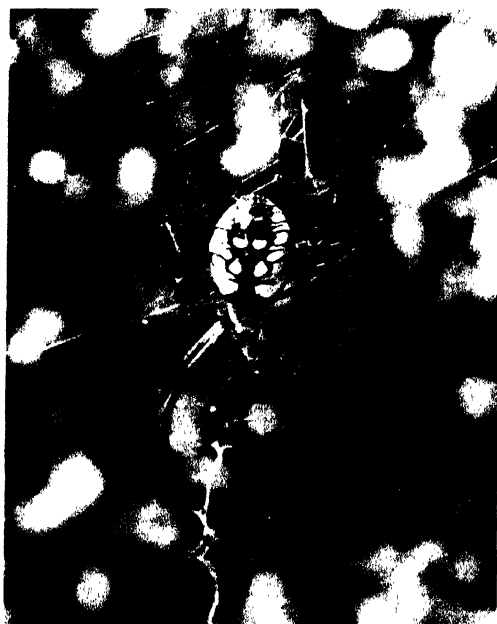
This highly interesting but bizarre class is singularly lacking in homogeneity. In it we find variations in size and form from the great king crab *Limulus* to microscopic mites (Fig. 310; see also Fig. 70, page 102). Despite their differences, arachnoids have common characteristics, probably signs of real phylogenetic relationship, for the class seems to have had a long period of independent evolution. The body of an arachnid generally consists of only two distinct regions, *cephalothorax* and *abdomen*. The headpiece or cephalothorax bears six pairs of appendages, four generally serving as walking legs. Of the other two, the first pair

are *mandibles*, and the second, the *pedipalps*, instruments for the manipulation of food. These are sometimes equipped with pincers. The abdomen, which properly corresponds to the thorax of an insect, seldom has appendages. Sometimes segmented and sometimes not, it contains the remarkable book gills or book lungs used by some types of arachnoids for respiration.

Sensory Equipment

The simplest members of the class are still marine, but almost all others have evolved into typical land animals, either with book lungs or with branched trachea. Eyes are usually simple ocelli, sometimes quite efficient, as one may verify by observing the visual alertness of the tigerish little jumping spiders that prey on flies during the summer. Hearing, or at least detection of vibrations, may be acute, though tonal discrimination is probably lacking. The chemical senses are perhaps limited to taste, for arachnoids lack antennae, which are important to the sense of smell in insects. The arachnid pattern of activity appears to be

Fig. 309. Garden spider, *Miranda aurantia*, in the middle of its web. This specimen was found near Calistoga, California.



much like that of most other invertebrates in that it is largely automatic or controlled by instinct, though some latitude of adaptation is possible.

Kinds of Arachnoids

The subclass Xiphosura, represented by *Limulus*, is primarily of historic interest, but this amply repays any effort spent in studying it. As we have seen, this living fossil, reminiscent of the ancient eurypterids and tracing back to the trilobites, is a remarkable anachronism.

All other arachnoids belong to the subclass Arachnida, of which the scorpions form the first order. These prowlers of the night are surpassed only by *Limulus* in their ancient lineage, some having come down from the Silurian with little change. They are characterized by a long, segmented abdomen with a poisonous curved sting at its tip. Normally curled up over the back, this fearsome weapon is ever poised to strike, and under suitable circumstances has been said to cause death even to man. Closely related to the true scorpions are the minute pseudoscorpions, often no larger than a sand grain. These may sometimes be seen sidling over the pages of a dusty book in search of still smaller mites.

Another group, the Phalangida, deserves mention only because one of its least obnoxious members, the harvest-man or daddy-long-legs, is familiar to everyone.

Spiders and Their Webs

The largest, most highly evolved and apparently most successful order of arachnoids is the order *Araneida*, the true spiders. Found almost everywhere on earth, they range in size from giant bird-catchers (*Avicularia*), measuring over three inches in length, to minute creatures almost microscopic in size. Perhaps the most characteristic and striking habit of spiders is web-weaving, which is not, however, shared by all, nor is it exclusively a spider talent. However, nothing in the structure or habit of a spider more characteristically illustrates the



Fig. 310. Land mite (actual size $\frac{1}{4}$ inch) lives in open fields.

amazing specialization of these creatures.

A filament of spider silk is not at first sight striking, but it is remarkable that a creature can unroll yard after yard of silk from a seemingly inexhaustible internal supply. At the tip of the abdomen, a spider has two or three pairs of protruding structures, each studded with as many as a hundred microscopic nozzles of varying sizes, called spinnerets. These lead from glandular structures that all but fill the abdomen, silk-secreting glands differentiated in shape and producing different qualities of silk, each kind adapted to an essential need of the spider. As many as five different kinds of threads may be produced. A thread is produced as a sticky, viscous stream of liquid which hardens on contact with the air, in exactly the way modern man has learned to form the threads of rayon or nylon, which he manufactures by extruding viscous plastics through fine holes.

In spinning its web, the spider can produce hard, strong filaments, or sticky, mucilaginous



Fig. 311. Ticks, carriers of relapsing fever.

threads for cementing the former to a fixed object, or tacky threads covered with thousands of microscopic beads of adhesive. Threads may be made thicker or thinner by the use of more or fewer spinnerets, and the spider unerringly produces the right kind of thread for the job in hand. The framework of the web is constructed of multiple strands of non-sticky threads, while the intricate net proper has sticky strands woven into it which form an effective insect trap. Web construction is a major feat of engineering and should be seen at first hand — as it easily can be on a summer morning. The spider's various legs are specialized tools for different steps in the construction, and the professional manner in which a spider weaves its first net, without benefit of sample or tutor, has not yet been explained. Though a spider usually performs its weaving by a set pattern, suggesting simple reflex or instinctive behavior, this is by no means always so. The sequence of building is not in all cases identical, and each web-site presents slightly different problems. We still have much to learn in our own backyard.

Mites and Ticks

Of all arachnoids, the degenerate and often parasitic mites and ticks show the most varied modes of living. Free-living forms may be found under rocks, in the soil, under the bark of trees, on leaves, in streams, and in the ocean. Parasitic forms are found attached to virtually any and every kind of animal, vertebrate and invertebrate. Here they cause annoyance and not infrequently death, since they may transmit diseases such as African relapsing fever, Texas cattle fever, and Rocky Mountain spotted fever, deadly to man or his domestic animals. Many of the mites which live on plants are serious agricultural pests. Among the amazing life-habits of some of them is the mating of young males and females with one another while they are still within the brood pouch of the mother, that is, before they are actually "born."

THE INSECTS

Of all the known species of animals, some three quarters are arthropods. Since nine out of ten arthropods are insects (class *Insecta*), the vast diversity of this group is apparent. Add to this the enormous fecundity of the individual insect, and the overwhelming magnitude of their numbers stands out as one of the most impressive single facts in the story of life. A single anthill may number millions of individuals. Insects swarm in every conceivable corner of the earth, in the water, and on the land. Only the ocean has remained practically closed to them, and here the crustaceans play the role that insects play on land.

The Insects as Competitors

It is perhaps fortunate that certain features of insect anatomy, such as tracheal breathing and the exoskeleton, have restricted insects to a relatively small size, for it is doubtful that many other forms of life could otherwise compete with them. Despite their small size — few exceed six inches and some are no more than .01 inch in length — they are competitors

and foes to be reckoned with, and it is not possible to say that man's struggle with them will always be successful. In this country alone, millions of dollars are spent annually to keep insect destruction to a bearable minimum. Despite the introduction of new chemicals in our warfare with insects, the struggle becomes ever keener.

The principle of evolution should prepare us to expect this, for their enormous reproductive rate causes population pressures that result in rigorous selection, and so pave the way for speedy evolution. Organisms with a low rate of reproduction can produce fewer total mutations, and since mutations are the raw material of evolution, the evolution of such creatures must be slower for that reason, too. The number of insect species gives evidence of their highly successful evolution and rapid adaptation to changes in their environment. Recent experiences in man's struggle against insects that attack his food crops point up this truth. For insecticides that once destroyed insect pests on fruit trees appear to lose their effectiveness in the course of time.

The mechanism at work is not hard to imagine. Among the millions of insects in an orchard, there will be many variants, and some will by chance resist specific poisons. Fumigation of the orchard will inevitably leave survivors — some because of the chance distribu-

tion of the poison, others because they may have a greater tolerance for it. These more resistant individuals will produce a large part of the next generation that will have the same high resistance. Under conditions favorable for the insect, this unwitting selection may ultimately produce a breed capable of surviving in the face of a poison that was once a satisfactory control. Thus, species of scale insects that attack citrus trees in California have, in some regions, produced mutant forms resistant to concentrations of hydrocyanic gas that once killed nearly 100 per cent of them.

The problem of the insect as man's competitor becomes vastly more difficult and complex because we cannot afford to destroy insects totally. We could well afford the total destruction of certain species, but unfortunately most of our potent weapons are fatal to many species, including those which are indispensable — especially various kinds of bees. It must be remembered that many of our higher plants are dependent upon insects for pollination. Their destruction would end the reproductive activities of these plants, and it is difficult to see how any practical substitute could be found.

General Characteristics

In addition to the common characteristics of the arthropods, all insects have the distin-

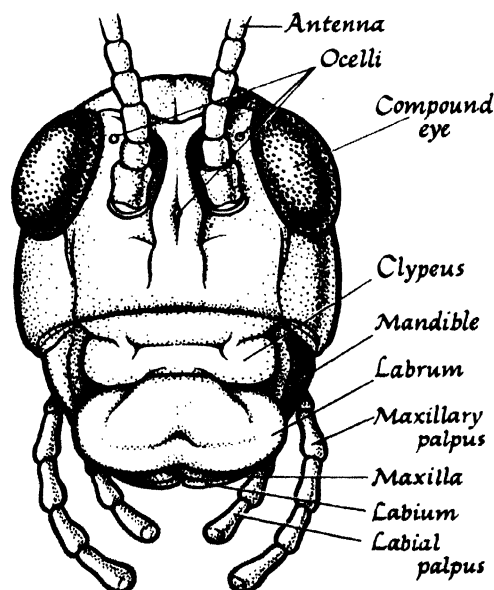
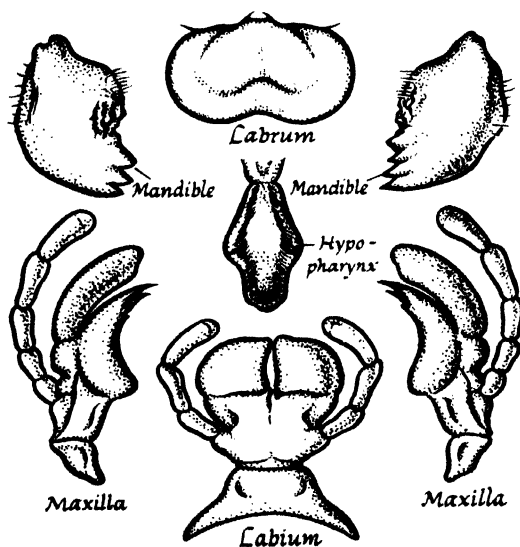


Fig. 312. Grasshopper, head and mouth parts.



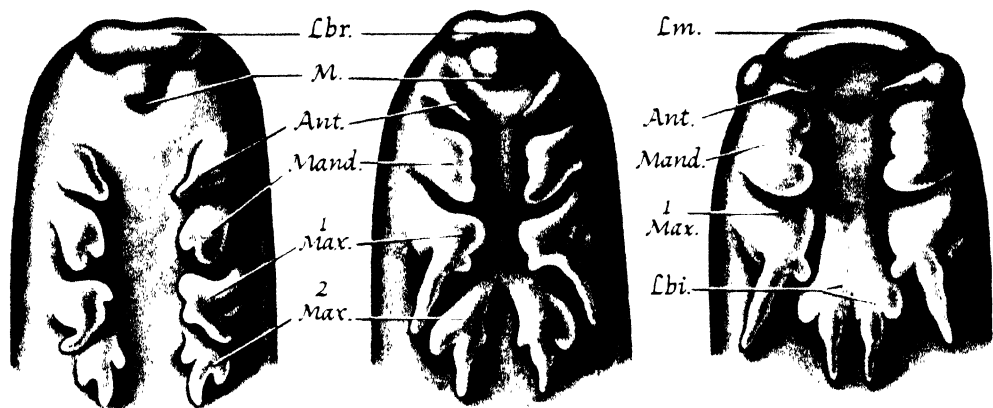


Fig. 313. Embryonic origin of the head-appendages of an insect (*Hydrophilus*). *Lbr.*, labrum; *M.*, mouth; *Ant.*, antenna; *Mand.*, mandible; *1 Max.*, first maxilla; *2 Max.*, second maxilla. Second maxillae fuse to form *Lbi.*, labium.

guishing features of their class. The body is in three sections, head, thorax, and abdomen. Six fused segments generally form the head, three the thorax, and eleven the abdomen, though here there may be fewer. As in crustaceans, the appendages are homologous; all are modified "legs," except probably the wings.

The Insect Head. The head of a grasshopper is typical of insect heads, in general (Fig. 312). In addition to a pair of compound eyes, there are three median ocelli. A pair of antennae and three pairs of other appendages transformed into chewing mouth parts are developments of the arthropod leg. In different insects the mouth parts are almost endlessly varied as highly specialized organs for obtaining food. At first glance the lapping mouth of a fly or bee and the piercing mouth of a mosquito look quite unlike the chewing mouth of a grasshopper. Yet all these mouth parts have been derived from the same number and kind of head appendages.

These parts consist of three paired structures aided by median unpaired ones. The first pair is the *mandibles*, the second the *first maxillae*, and the third the *second maxillae*, the last always fused to form a structure called the *labium* or lower lip. The upper lip, or *labrum*, is not derived from paired appendages. In embryonic stages, the origin of the mouth parts, as of the antennae, is quite clear (Fig. 313). Of particular interest is the manner in which the

second maxillae fuse to form the labium. Chewing mouth parts, such as those of the grasshopper, are considered the primitive form, since insects with sucking or piercing mouth parts have larvae equipped for chewing, *e.g.*, caterpillars, the larvae of butterflies. Further evidence of the origin of the mouth parts is seen in the sensory processes of the maxillae, the *palps*, which look somewhat like degenerate legs.

Transformation of chewing to sucking mouth parts probably came about independently in different groups and arose from a variety of structures. The intricacy and effectiveness of such modifications may be appreciated by comparing the mouth parts of the grasshopper with those of a mosquito (Fig. 315). That so minute a creature can pierce the leathery skin of a human being with such a delicate structure almost defies belief.

The Insect Thorax: Legs and Wings. Three segments form the thorax or mid-section, each segment having a pair of legs and the last two usually wings as well. The legs are immensely varied (Fig. 314), though all built on the same pattern, so clearly shown in the leg of the grasshopper. The oars of the water boatman, the trap-like front legs of the mantis, the digging legs of the mole-cricket, and the sticky clinging legs of the housefly are all modifications of the same original appendage. There are also great differences between the pairs of legs of the same

individual, for they serve different purposes.

Wings are chitinous folds of the body wall, with nerve and tracheal branches from the coelom. These form the veins of the mature wing, which after it has attained full development becomes a lifeless appendage, moved by muscles in the thorax. The origin of the insect wing is uncertain. It shows no relationship to the legs, and may have evolved from chitinous scales, first used by leaping insects to prolong their leaps. Although no insects today possess more than two pairs of wings, certain fossil insects of the Carboniferous period show rudiments of wings on the first segment of the thorax, too. In certain insects, such as the flies, mosquitoes, and midges, the wings of the third segment of the thorax have become modified into knob-like structures called *halteres*, which, whirling like gyroscopes, have a balancing function. Among wingless insects, some of the simple orders have presumably never had wings, the absence of which is to be considered a primitive condition (Fig. 319). Others, quite obviously descended from winged forms, have lost their wings in the course of evolution. Thus ants and termites are wingless except in their sexual phases. Other wingless insects show close relationship to forms that are winged. In still others, including some butterflies, only

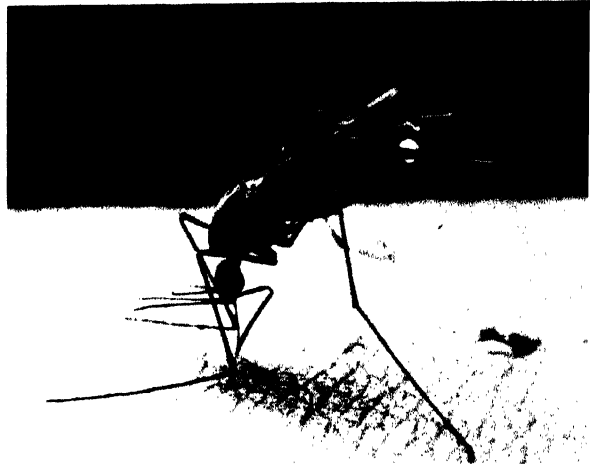
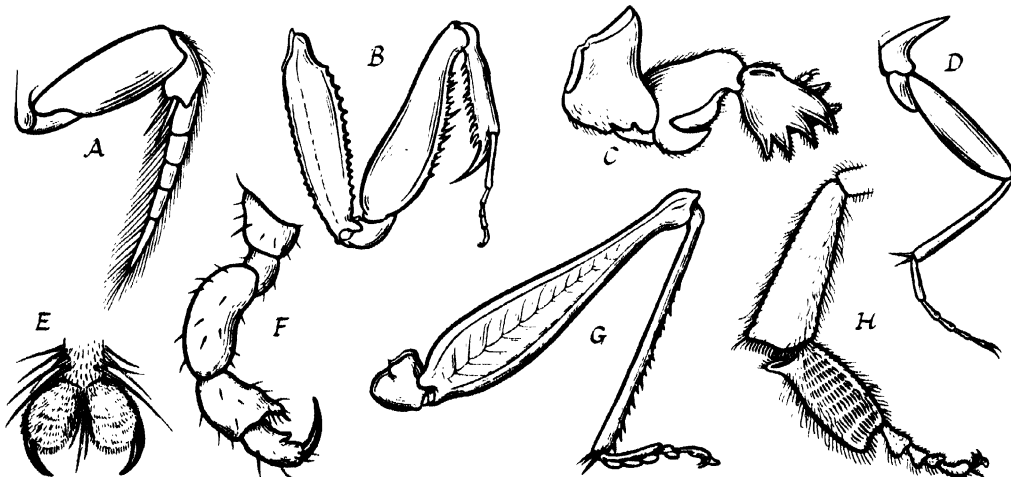


Fig. 315. Mosquito puncturing a human hand.

males have wings. An intermediate stage in the evolution of this peculiar dimorphism is evident in the sluggishness of some winged females, a sluggishness which seems to be associated with increased weight due to the eggs they carry. Males mate more readily with the less active females — perhaps this was the selective force which has produced entirely wingless forms.

The Insect Abdomen. Fully developed legs are absent from the abdominal segments of adult insects. In some primitive forms (Fig. 319), there are segmented processes on the abdominal segments which may be vestiges of

Fig. 314. Legs of insects are modified for many functions. *A.* A paddle — the hind leg of the water beetle. *B.* A grasping organ, the fore leg of the praying mantis. *C.* The digging fore leg of the mole cricket. *D.* Hind leg of the ground beetle, for running. *E.* The foot of the housefly has claws and sticky climbing-pads. *F.* The fore leg of the head louse is adapted for grasping hair. *G.* Hind leg of the grasshopper, for leaping. *H.* Left hind leg of worker bee, for collecting pollen.



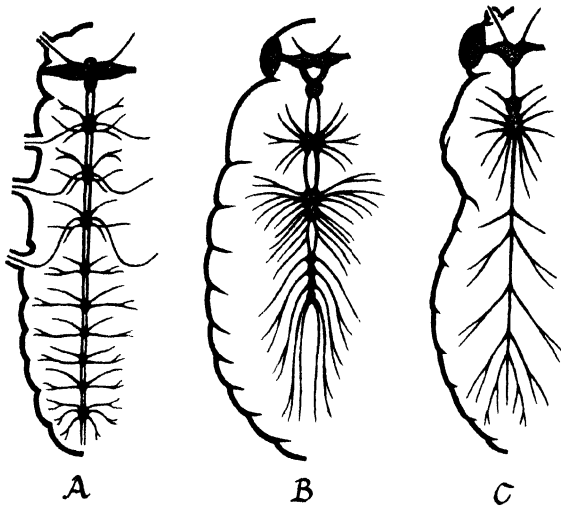


Fig. 316. Nervous systems of insects show increasing condensation and fusion in more highly evolved types. A. Termite. B. Water beetle. C. Fly.

abdominal legs. Other bristle-like appendages often found on insects may be similar remnants. The familiar "legs" on the abdominal segments of caterpillars differ basically from typical arthropod appendages, for they are fleshy and unsegmented. But they show an interesting similarity to the fleshy, bristle-bearing protuberances of some polychaete annelids and to the legs of *Peripatus*: a case of larval similarity to more primitive related forms.

Internal Organs. In details, the structure of the insect's digestive tract varies as widely as its food habits, though in general it is enough to differentiate between chewing and sucking types. The main difference between these two is that the latter have a bulb-like muscular pharynx, which serves as a suction pump, while the chewing insects lack this but have a muscular gizzard lined with chitinous grinding teeth. Variations in detail and differences in length produce systems of quite different appearance. There may be glandular and absorptive *gastric caeca*, or pockets, and there is always an intestine ending in a rectum.

Fine thread-like processes, the *Malpighian tubules*, which empty into the anterior part of the intestine, are excretory organs. The tu-

bules lie within the hemocoel and are thus bathed in blood, from which they remove a soluble nitrogenous waste, uric acid.

The circulatory system is similar to that of the crayfish, but somewhat cruder. It consists of a tubular heart in the dorsal body cavity, surrounded by the hemocoel. Blood is pumped through arteries which end abruptly in sinuses in and around the various organs, and returns to the heart by way of the hemocoel, aided and directed by various partitions so that it follows a definite course despite the lack of further arteries or veins. This system is far less complex than that of the vertebrates, but must be adequate for so small an animal and for its sole function of distributing food stuffs and chemical regulators, and of collecting wastes.

The respiratory system consists of an intricate network of air ducts (tracheae), in some insects developed into large air sacs. Air is taken into these through openings in the thorax and abdomen and is thus piped throughout the body. The blood is consequently relieved of carrying oxygen and carbon dioxide, as it must do in organisms with highly localized respiratory systems, such as the air breathing vertebrates.

Nervous System, Motion, and Perception. There is a ventral double nerve cord, much like that in the crayfish. In primitive insects and larval forms each segment has a ganglion, but in more complex forms and in adult insects, ganglia tend to merge, until in the true bugs (Hemiptera) all the abdominal and thoracic ganglia are fused into a single mass (Fig. 316).

Organs of perception are much like those in the crustaceans, though in addition to eyes, antennae, and sensory bristles, insects also have auditory organs. These may be of various origins and are independently evolved, like the various sound-producing organs. Ears may be found in the antennae, on the first abdominal segment, or upon the legs.

As in the Crustacea, internal muscles are fastened to the chitinous exoskeleton. In proportion to its size, an insect can perform feats of strength and endurance quite beyond the range of any mammal. An ant, carrying an ob-

ject exceeding its own weight, can run up a vertical wall at an amazing speed. Roughly, this would be equivalent to a human being climbing a vertical cliff at about twenty miles an hour carrying a weight of two hundred pounds.

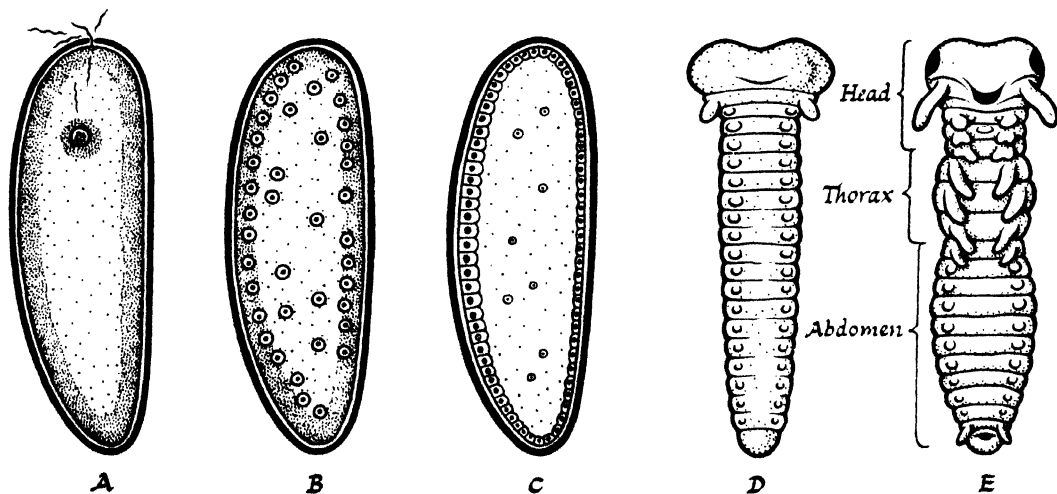
Reproduction. Insects, like crustaceans, reproduce sexually, and the sexes are always separate. Eggs are fertilized internally. There are many different kinds of accessory appendages for copulation and egg depositing, and some forms are parthenogenetic. But in other respects, insects differ almost as much in reproductive processes as in appearance. As might be expected in such highly evolved organisms, the entire physical and nervous resources of the adult animal are often devoted to producing the next generation or preparing conditions for its successful emergence. The life of a honey-bee, for instance, is one continuous process of raising the next generation. In many forms, the adults die immediately after mating and egg-laying. The famous silkworm moth, for instance, has such rudimentary mouth parts that it is unable to eat at all after it hatches from the cocoon.

The eggs of insects undergo a superficial cleavage that differs considerably from the process in the annelid egg (Fig. 317). The diploid nucleus which results from the fusion of

egg and sperm nucleus divides repeatedly, producing many free nuclei scattered throughout the cytoplasm. These migrate to the periphery and there produce a single layer of cells, a yolk-filled blastula. Segments and tissues then develop. Three segments are incorporated into the head to begin with, and later three others produce the mandibles, the maxillae, and the labium.

Metamorphosis. The eggs of most insects hatch into larval forms, though some have no larval stage and some show little change from larva to adult. Most insects, however, pass through a revolutionary metamorphosis. Like that of crustaceans, insect development is largely determined by the fact that most growth takes place in sharply marked phases with the periodic molting of the exoskeleton. And since no newly hatched insect has wings, the larvae of highly specialized flying insects differ markedly from the adults in appearance, habit, and frequently in diet. According to mode of development, insects are of three types: (1) those having no metamorphosis, (2) those with incomplete metamorphosis and relatively little difference between larva and imago (sexually mature winged state), and (3) those with a marked difference between larva and imago, separated by an inactive pupal stage.

Fig. 317. Embryology of an insect. *A*. Fertilization. *B*. Cleavage nuclei scattered throughout cytoplasm migrate to periphery of egg. *C*. Cell walls appear between nuclei, producing a single layer of cells. *D*. Segmentation develops. Three segments are involved in forming the primitive head. *E*. Mandibles, maxillae and labium are produced. Three additional body segments are incorporated into the head. The body appendages become the two pairs of maxillae and the labium.



Viewed in the light of evolution, the life history of a completely metamorphosing insect is an absorbing story. The ancestors of insects were unquestionably "worm-like," and there are clear vestiges of these ancestors in the larval stages. Moreover, since an insect larva lives in a different environment than the adult, it is subject to different selective factors. Hence the two are likely to diverge still further. There are indeed enormous differences in some varieties — witness maggot and fly, grub and beetle, caterpillar and butterfly, in which almost every detail of structure is different.

The extent of the differences between larva and imago helps to explain the pupal stage. This is the stage that follows the last molt of the larva, and in the most highly specialized metamorphoses involves complete reorganization of tissues and structures, so that much of the pupa consists merely of loose masses of cells. Yet the structures of the imago do not arise as suddenly as appearances may suggest. While a caterpillar has no wings, it has wing buds which grow with every molt. These buds are little humps or folds of the skin, not readily apparent because they are hidden in pockets beneath the surface, their openings tiny or completely closed over. Pupae vary in degree of immobility. Some crawl or swim, like the mosquito pupa, which wriggles through the water, or the grub-like pupa of the June bug which feebly burrows in the ground. Pupae of butterflies can only move their abdominal regions slightly, while others, such as those of

flies, become so encased that they lose all power of motion.

The most primitive insects undergo no metamorphosis. Grasshoppers are intermediate, and butterflies undergo complete metamorphosis.

PRINCIPAL INSECT GROUPS

The more than 700,000 species of insects are usually grouped in about twenty-six orders, though sometimes more or less. The following are some of the commonest and most important ones and those of special evolutionary interest. A complete listing will be found in Appendix A.

Protura (Gr. *pro* = first). These are little known, tiny insects, primitive in structure. In addition to thoracic legs, they have three pairs of leg-like abdominal appendages. Segmentation is uniform. There is no real metamorphosis, no wings, compound eyes, or antennae. They are found all over the world in moist soil and under bark and stones (Fig. 319).

Thysanura (Gr. *thysanos* = tassel + *oura* = tail). These are primitive, wingless insects, like the silverfish, often found in moist places such as kitchens and bathrooms. Mouth parts are equipped for chewing. They do havoc in libraries among the books. There is little differentiation of segments and no real metamorphosis (Fig. 319).

Orthoptera (Gr. *orthos* = straight + *pteron* = wing). Many common insects — about 30,000 species of grasshoppers, katydids, crickets, cockroaches, and so on — are of this group. The fore wings are generally leathery and straight; the hind wings are pleated. Mouth parts are chewing. Metamorphosis is incomplete and the larval forms (nymphs) are terrestrial. Except for the grotesque mantis, most orthopterans are vegetarian and are thus our competitors or enemies: the scourges of locusts — migratory grasshoppers — is an example. The cockroach, if not a menace, is certainly a pest. It is also one of the oldest and most successful of insect types, giant cockroaches having lived in the Carboniferous period.

Isoptera (Gr. *isos* = equal + *pteron* = wing). The termites or white ants are primitive in structure but have evolved a truly remarkable

Fig. 318. A grasshopper, one of the Orthoptera.



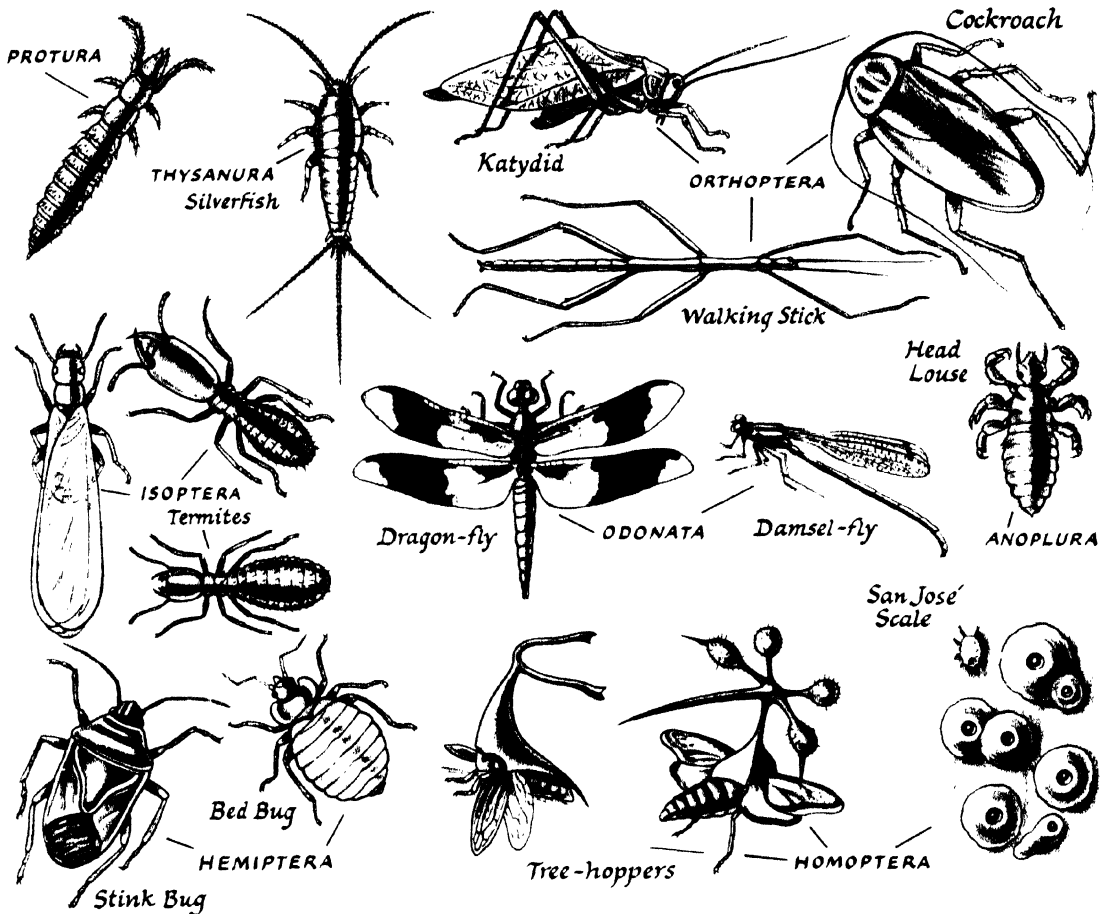


Fig. 319. Representatives of some insect orders. (Specimens not to same scale.)

social organization. Wings generally are similar, and the mouth is adapted for chewing. Metamorphosis is incomplete. Attacking wood and wood products, they are a serious menace to buildings. Termites shun light, and if wood is not accessible by direct contact with the ground or through tunnels, it will not be attacked. The ability to digest wood is known to depend upon the presence of symbiotic protozoa in the intestinal tract. Termites are polymorphic and have four castes: a winged reproductive caste; a wingless reproductive caste; workers, male and female; and soldiers, male and female (Fig. 319).

Odonata (Gr. *odous* = tooth). These are the common and well-known dragon and damselflies. The dragon flies have four large membranous wings, immense compound eyes, and chewing mouth parts. They are strong fliers

and destroy mosquitoes. Metamorphosis is incomplete, but the aquatic nymph is not very similar to the imago. Like the adult, the nymph is a voracious predator. It has an enormous labium that folds under the head and can be shot out like a pair of tongs to catch unwary prey, and it travels by the original instance of jet-propulsion — shooting a stream of water rapidly from its rear end. Damselflies are weak fliers and their wings are folded over the body when not in flight. Their bright metallic colors are often seen at the margins of ponds and swamps (Fig. 319).

Anoplura (Gr. *anoplos* = unarmed + *oura* = tail). These, the true lice, are wingless and parasitic, with mouth parts specialized for piercing and sucking and with no metamorphosis. Their parasitic mode of life has brought about considerable degeneration of structures

rendered unnecessary. Ocelli are lacking and compound eyes are vestigial. Three forms of lice attack the human species, the head louse, the body louse or "cootie," and the crab louse, which affects armpits and pubic regions. Other members of this order attach themselves to dogs, horses, cattle, and other animals. They transmit the germs that cause such diseases as trench fever and relapsing fever.

Hemiptera (Gr. *hemi* = half + *pteron* = wing). So named because the lower half of the front wings is leathery and their membranous ends overlap on the back, thus suggesting half wings, these are the true bugs. They vary considerably, but most of them are flattened and blunt in shape. Mouth parts, specialized for piercing and sucking, have a formidable beak on the forepart of the head. Metamorphosis is incomplete. While some kill harmful insects, many are harmful garden pests. Some are characterized by vile odors, e.g., the "stinkbugs." The chinch-bug has destroyed millions of dollars worth of grain. The common bedbug is also of this group.

Not a few Hemiptera are aquatic. *Belostoma indicum*, indigenous to India, measures over three inches in length and even preys on fishes that exceed it in size. The common water striders, or skaters, dance upon still summer pools without wetting their feet. Their close relative, *Halobates germanus*, one of the rare insects that dare go to sea, has been found walking upon the water five hundred miles from land.

Homoptera (Gr. *homos* = same + *pteron* = wing). Most of these insects have four wings of uniform thickness throughout, though in some the hind wings are reduced and others are wingless. Because of their great diversity of shape, despite really similar structure, no single common name applies to all members of this pestiferous order. It includes the cicadas — popularly misnamed locusts — various leafhoppers, the aphids, and the various scale insects. Mouth parts pierce and suck, and metamorphosis is generally incomplete (Fig. 319).

This order includes the most bizarre shapes of the insect world. The tree hoppers make a

wild display of horns, clubs, spikes, balloons, and thorns, without apparent function. Others show striking forms of mimicry. Some simulate grasshoppers; others, butterflies and moths. Important because of the damage their great numbers do to plants are the plant lice or aphids. These are of many forms, sizes, and colors. Some protect their bodies with white waxy threads that give them a woolly appearance and cause them to be called *woolly aphids*. Many produce a sweet secretion called honeydew, which covers the leaves of plants with a sticky varnish upon which fungi grow, blackening the leaves. For this honeydew, ants protect aphids and provide for them as the farmer provides for his milk cows, even transferring them to fresh pastures. The crowning pest of this group is the San Jose scale, a serious threat to orchards in many parts of this country.

Coleoptera (Gr. *coleos* = sheath + *pteron* = wing). These are the beetles, by far the most numerous in species among the insects (ca. 300,000), easily recognized by their chitinous front wings, which form a shield over the membranous back wings. Mouth parts are for chewing, and metamorphosis is complete. Although some beetles are excellent fliers, others lack hind wings, and the front wings serve only to protect the body. Some are gigantic, for insects, while others are minute. Many are serious pests. Among these are the potato beetle, the Japanese beetle, the June bug, the rose-bug, the flea-beetle, and the cotton boll weevil (Fig. 320).

Lepidoptera (Gr. *lepidos* = scale + *pteron* = wing). The wings of moths and butterflies are covered with microscopic scales which give them their velvety patterns. Four wings are characteristic, although a few species are wingless. Metamorphosis is complete. Mouth parts are specialized for sucking, but in some are vestigial, since many adult moths do not eat. The larvae are popularly called caterpillars (*L. catta pilosa* = hairy cat), though not all are hairy. Most caterpillars feed on vegetable matter, but a few have shifted to animal food, for example, the clothes-moth, which in its larval stage feeds on animal hair. The wax-

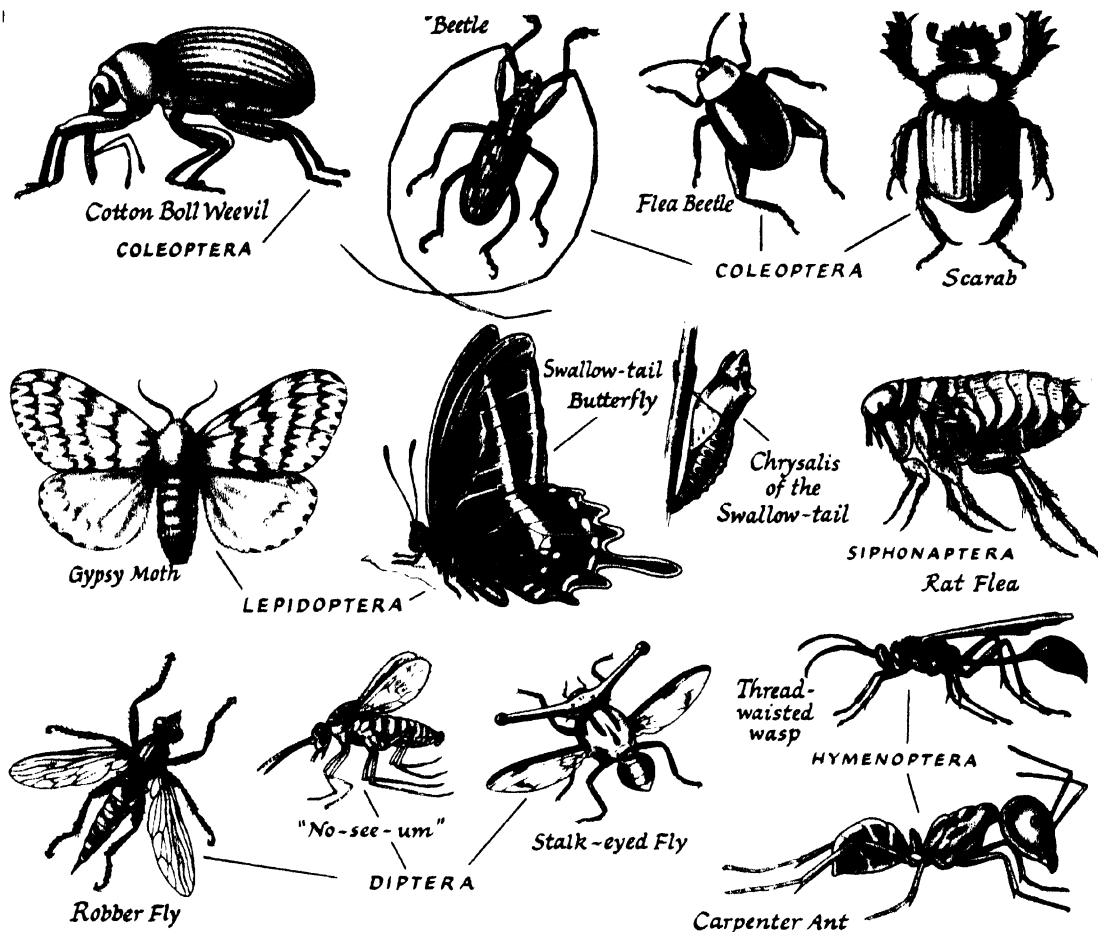


Fig. 320. More representatives of insect orders. (Specimens not to same scale.)

moth invades colonies of bees, chews up the combs, covers them with fecal matter and a mass of web and cocoons, and finally causes the death of the colony. Moths usually fly by night, and their wings are folded to the body when at rest. Butterflies are generally daytime fliers and their wings are usually folded vertically above the back when at rest (Fig. 320).

Beautiful as they are, the 150,000 species of butterflies and moths are a serious menace to the plants upon which man depends. Under favorable conditions they multiply at an enormous rate, and their larvae may denude whole forests and countrysides. Especially destructive is the gypsy moth, *Porthetria dispar*, a European species introduced into Massachusetts in 1866 by a French biologist who was experimenting on silkworms. Damage done by this moth alone runs to many millions of dollars

annually. Another import from Europe is the brown-tailed moth, introduced into Massachusetts and first appearing as a menace in 1897. The barbed hairs of its larva are poisonous, and exposure either to the larva or to its cast skin produces swellings like hives and intolerable itching. Well known are the community webs produced by the common tent-caterpillars. A similar web is produced by the fall webworm. Of inestimable damage to apple growers is the codling-moth, *Carpocapsa pomonella*. The worm head that waves from the core of a wormy apple is its larva. The European corn-borer, *Pyrausta nubilalis*, bores into young ears of corn, making them unsaleable and inedible. The worm also attacks the hollow stems of other garden plants.

Of the whole group only the silkworm, *Bombyx mori*, has contributed to human welfare.

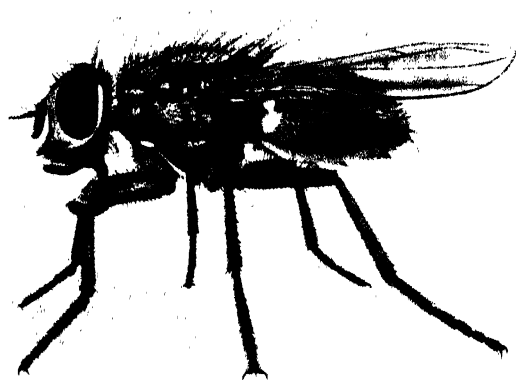


Fig. 321. The housefly, one of the best known of the Diptera.

Balance in nature is delicate, and any interference with it hazardous. Still it appears that if it were given us to eradicate all Lepidoptera, we would benefit greatly by doing so. But romance and the love of beauty defend the charming, gay butterflies and great, soft-winged moths.

Diptera (Gr. *dis* = two + *pteron* = wing). These are the flies, midges, and mosquitoes, nearly 100,000 species with mouth parts equipped for sucking, and with a complete metamorphosis. They have, of course, only two wings, the hind wings being replaced by halteres. Biologically the Diptera is a very successful group, but pests! It can be said in favor of them, from the standpoint of man, only that some feed on other insects and some act as scavengers by eating dead organic matter; while without *Drosophila* we might still know very little about heredity. Among those which especially affect man are the mosquitoes, including the common mosquito, yellow fever mosquito, malaria-carrying *Anopheles*, and others. The flies include among others the common housefly and the tsetse flies of Africa, carrier of the nagana disease of cattle and also carrier of the causae of sleeping sickness. Botflies spend their larval life as parasites within the bodies of domestic animals such as sheep and cattle, making holes in their skins and

ruining their hides. The blow-flies include the common large steel-blue blow-fly, *Calliphora vomitoria*, the larvae of which develop in decaying meat; and the greenbottle fly, which lays its eggs in open wounds that then become infested with maggots, the larvae. A midge commonly known as "no-see-um" — said to have been so named by the Indians because of its minute size — bites viciously and sucks blood. The robber flies are large predacious flies which destroy other insects (Fig. 320).

Siphonaptera (Gr. *siphon* = tube + *aptera* = no wings). These are the fleas, laterally flattened insects with siphon-like sucking tubes and without wings. The larva — small, hairy, and worm-like — has biting mouth parts and feeds upon decaying organic matter. The adult is parasitic and lives on the blood of its host. Under reasonably sanitary conditions the flea is no great menace, but it may become a serious one as a carrier of bubonic plague. Although fleas — there are only about 1000 species — generally prefer one kind of animal, they may temporarily put up with a substitute host. It is this occasional shifting that makes them especially dangerous as carriers of disease, as from rat to man. Best known are the human flea, *Pulex irritans*; the cat flea, *Ctenocephalus felis*; and the dog flea, *Ctenocephalus canis*.

Hymenoptera (Gr. *hymen* = marriage or union + *pteron* = wing). These are the bees, wasps, and ants. Mouth parts may be adapted for chewing only, or for chewing and sucking, as in the bees. Females are usually equipped with a sting or piercing ovipositor. Metamorphosis is complete. The front and hind wings are neatly locked together by a row of hooks on one wing that fit into a groove on the margin of the other (Fig. 320).

The Hymenoptera is almost the only prominent order of insects which man may consider as being valuable allies rather than competitors. Despite the several pests among this group that attack fruit trees, such as the saw-fly larva and certain ants, most of the 100,000 kinds of hymenopterans are all but indispensable to human life.

There are great numbers of parasites among

them, some with phenomenally specialized reproductive cycles delicately adapted to the host, usually another insect which conflicts with human interests. The table could easily be turned, and forms valuable to man could, however, become the victims. Parasitic hymenopterans generally lay eggs in or on the host, and the larvae then bring about its destruction. Many insects, such as caterpillars and aphids, are thus parasitized.

Ants are often thought of as annoying pests, but without them other insects would so increase in numbers as to threaten man's very existence. Most ants feed on animal tissues, and a single ant colony may destroy many thousands of adult insects, larvae, and eggs in a single day. Of all insects, the ants are the dominant type.

THE HONEYBEE

It is all too easy to accept the delicate mechanism of any living organism as just another group of facts — that it has six legs, four wings, sucking mouth parts, and so on. We are prone to accept these facts without much thought. But let us try to see the honeybee with a somewhat fresher eye.

Here is a creature smaller than the end of your little finger, an insignificant unit in a complex society of thousands like itself. But it is a perfect cog in the machinery of the hive and automatically does what it must do so that the hive will prosper. Tucked away within it are the physical and nervous mechanisms that enable it to move and act with precision, to produce special chemical substances, to manipulate these at the proper time and in the proper way. It can propel itself through miles of space at great speed, respond to the stimulus of light in such a way as to go toward sources of food substances vital to itself and to the hive. It can scent faint traces of aromatic substances in the air and respond positively or negatively to them, as the welfare of its hive demands that it should. Without previous experience, and solely under the guidance of its innate structure, it knows where to alight, how to enter a blossom, what to do when it gets there. It

gathers what is needed, automatically and unerringly, and returns over the miles to the spot it came from. Back in the hive, it deposits its pollen and regurgitates the nectar it has gathered, now chemically changed. If wax is needed, it suspends itself near the top of the hive where it is warmest, and slowly special gland cells on the underside of its abdominal segments manufacture thin and delicate wax plates. It cannot know why it is doing this any more than the other workers know why they visit the suspended one to gather the wax it has produced. No engineer could make a machine to perform as the bee performs. And yet, twenty-four days after the queen places an egg in a brood cell, such a creature emerges, an ordinary worker bee, beside whose structures and operations a delicate watch seems as crude as a stone slab stuck in the ground for a sun dial.

External Anatomy

The general insect characteristics found in the bee need not be reviewed, but there are many special features (Fig. 322). The two wings on each side are hooked together in flight so that they function as one. In addition to the large compound eyes are three simple ocelli on the top of the head.

Specialization of the Legs. The legs are a whole kit of complicated tools of the trade. The work of the bee is often dusty, for pollen is fired at it many times during its visits to blossoms, and it must spend considerable time in grooming. So the first leg bears a special set of bristles, the *eye-brush*. Immediately below this is an *antenna-comb*, a semi-circular, brush-lined depression covered with a movable flap. The bee raises its leg, hooks the comb over the base of its antenna, and repeatedly draws it through the comb while the flap holds it down. This leg also bears a *pollen-brush* similar to the eye-brush but used to remove pollen from the body. The second leg has only two special tools, another pollen brush and a *spur*, with which scales of wax are picked from the abdominal segments where they are secreted. The third leg has three distinct tools, a *pollen*

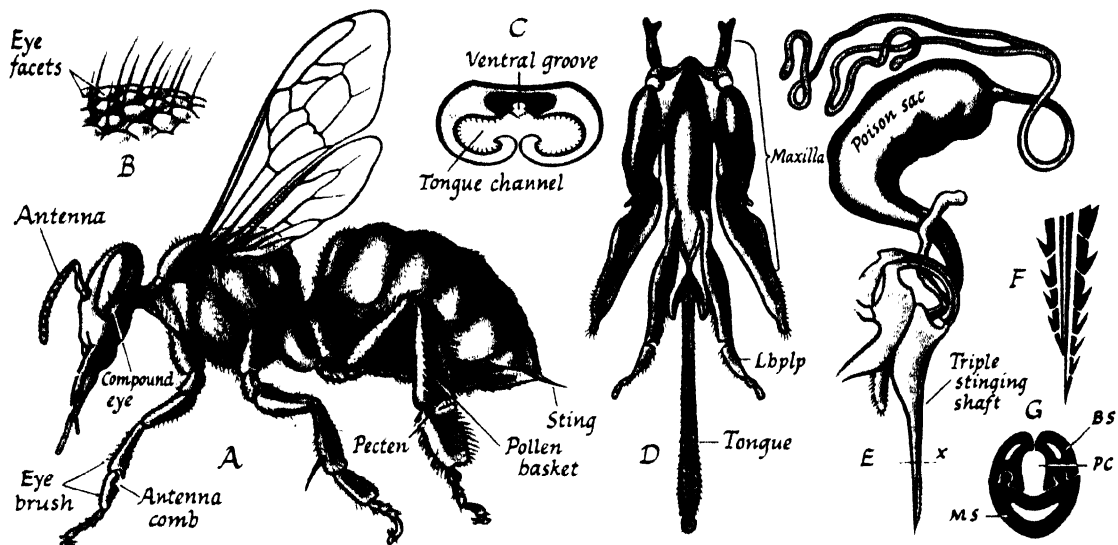


Fig. 322. Honeybee worker. *A.* Essential external features. *B.* Portion of compound eye. *C.* Cross-section of tongue. *D.* Mouth parts. *E.* Sting and poison mechanism. *F* and *G.* Tip and cross-section of sting.

comb, used to brush pollen from the middle legs and the rear portions of the body; the *pecten*, which scrapes the pollen out of the comb of the opposite leg onto the flattened upper part of the leg; and the *pollen basket*, a hollow, hair-covered depression into which, after a flexing movement of the leg has patted the pollen down into a compact mass, it is pushed. Great lumps of pollen can thus be built up, giving the bee an appearance of wearing bloomers of red, green, blue, or yellow. Besides serving as walking legs and landing gear, the legs of the honeybee are thus a kit of at least nine different tools.

The Mouth Parts. Modifications in the mouth parts of the bee have gone far beyond those in the grasshopper (Fig. 322). Labrum and mandibles show little differentiation, but the maxilla shows considerable change, and the labium has become complicated almost beyond recognition. Maxilla and labium together form a trunk-like *proboscis*, usually folded under beneath the head. Parts of the labrum are drawn out to form a long hairy "tongue" of opposed and interlocked U-shaped channels, that acts as a capillary duct for sucking up liquids. The *labial palps* form a sheath around this structure,

and are in turn supported by the sheath-like maxillae. The whole organ is an astonishingly complex and effective instrument for gathering droplets of nectar from the flowers which the bee visits.

The Sting. The modified ovipositor, the *sting* (Fig. 322), is far from the simple needle it appears to be. A bee attempting to drive its sting into a heavy glove performs a pumping action, and after some attempts, may get the point into the leather. If the bee is now brushed off with the free hand, it will probably fly off without its sting. This is fatal to the insect, for the sting is a large and complex mechanism, and its removal leaves a mortal wound. The abandoned sting continues to pump and bore quite independently of the bee, and may get its point through the glove long after the bee has departed. Actually, when the sting is torn out, the whole related mechanism of muscles, poison sacs, ducts, and barbed shafts goes with it. The sting itself is a needle composed of three parts, two barbed lateral shafts that slide within a groove on two rails of the stationary main shaft. In action, bunches of muscles alternately push down first one shaft and then the other. The barbs on one shaft anchor it in the

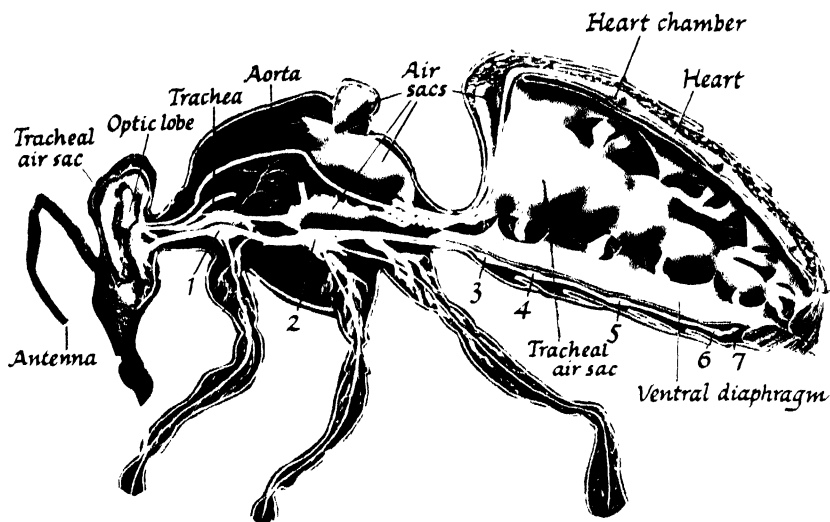


Fig. 323. Sagittal section of honeybee worker showing tracheal system, heart, aorta, and ventral nerve cord. 1-7, ganglia of ventral nerve cord.

tissue while the other is driven down, and so on. Venom is transmitted into the wound through a channel between these shafts.

Internal Structures

A honeybee takes in liquid food through its proboscis, though solid substances, such as pollen, may be passed directly into the mouth by the mandibles. Salivary glands in the head and thorax secrete softening and diluting fluids. From the mouth and pharynx, the food passes through a long, narrow esophagus into the *honey stomach*, which corresponds to the crop of other insects. No digestion occurs here; this is the "tank" in which the nectar is carried from the flower to the hive. A stalk-like tube connecting the honey stomach with the digesting stomach is kept closed unless the bee requires nectar or honey for its own use. These substances appear to be digested in the stomach, but pollen does not seem to be digested until it has passed into the intestine. The terminus of the digestive tract is the greatly distensible *rectum*. Bees do not discharge fecal matter in the hive, and since no flights are undertaken in the dead of the winter, all fecal matter is stored from late autumn until the first flight in early spring. This is possible because

of the relatively great purity and digestibility of honey, which leaves little waste.

The system of tracheae extends to the very tips of the legs, and large air sacs allow storage of sufficient air so that breathing during flight can be avoided (Fig. 323).

Reproduction. The reproductive system of the honeybee is highly specialized. Sperm cells, produced in the testis and stored in the seminal vesicles of the male, or drone (Fig. 324), are injected into the seminal vesicle of the queen at the time of mating and remain there until used, which may be several years later.

The enormous ovaries of the queen are masses of tubules within which the eggs may be seen at various stages of development, increasing in size as they move towards the oviduct. In the oviduct they pass the seminal vesicles, from which the queen may release sperm cells at will. During the brood-rearing season, the queen makes her way over the combs, examining the cells and introducing into each one the tip of her abdomen, with which she deposits a single egg that becomes cemented to the center of the bottom of the cell. This operation is repeated with almost clocklike precision every five or ten seconds, hour after hour.

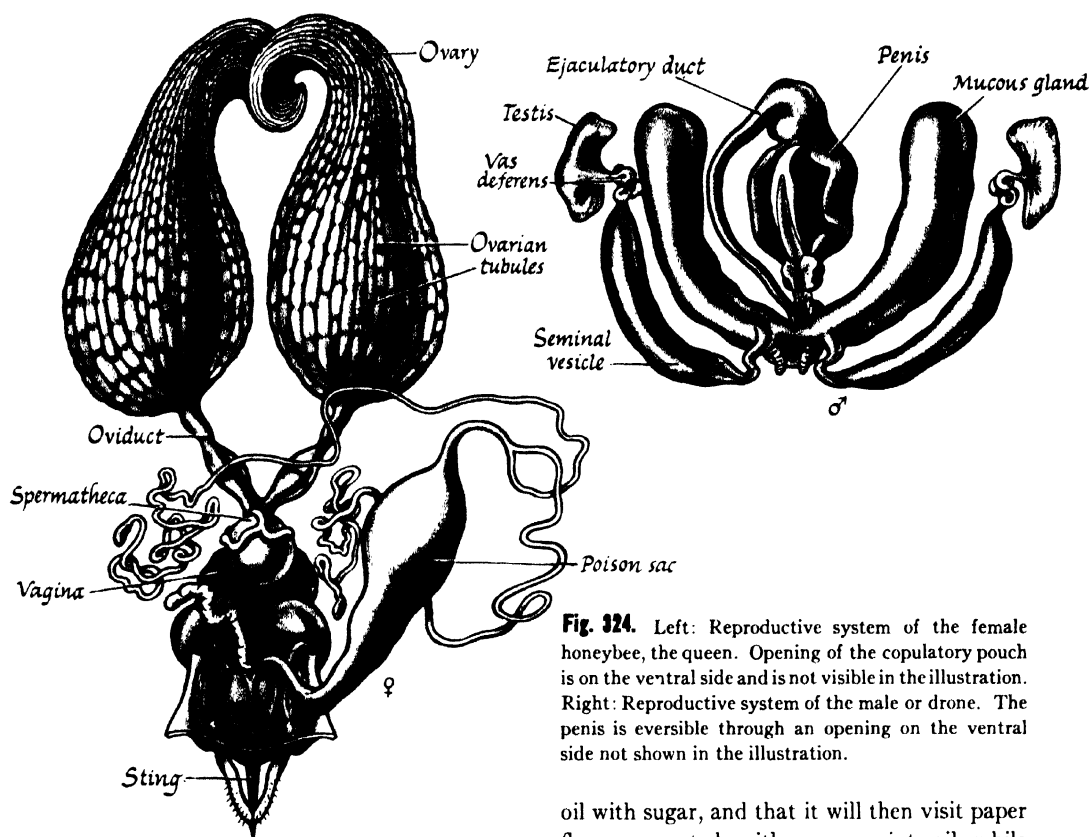


Fig. 324. Left: Reproductive system of the female honeybee, the queen. Opening of the copulatory pouch is on the ventral side and is not visible in the illustration. Right: Reproductive system of the male or drone. The penis is eversible through an opening on the ventral side not shown in the illustration.

Nervous and Sensory Organs. The nervous system is considerably centralized, and in the anterior part of the body the ganglia are much fused, the two main ones each consisting of three original ganglia. There are only two ganglia in the thorax, and five in the abdomen. Since coordination is largely controlled by the ganglia and movements are automatic, removal of the head does not greatly interfere with the coordination of the rest of the body, beyond removing most of the sensory directors located there: the eyes, the antennae, the organs of smell in the antennae, and some organs of taste.

Since behavior in the bee, as in insects generally, is basically automatic, training is possible only within the framework of relatively inflexible instincts. A bee may even be trained to react positively to odors not normally associated with nectar. The biologist von Frisch and others have shown that a bee may be trained to associate the smell of peppermint

oil with sugar, and that it will then visit paper flowers scented with peppermint oil while ignoring others not so scented. Bees also discriminate between certain colors. If bees have learned that flowers of a certain shade always have sugar solutions at their base, then only flowers of that shade will be visited, even if sugar solutions are removed from them. But within the hive, the bee appears to be an absolute automaton, and the development of the modern hive, in which individual combs are built in separate removable frames, was made possible only by obtaining the most exact information concerning bees' ways.

Bees were of course originally wild, and honey could be obtained only by felling and plundering the hollow tree in which they had established themselves. Later, it was discovered that bees could be transferred to artificial hollow logs, and still later these were replaced by large thimble-shaped straw tubs or "skeps" (Fig. 325). To obtain honey from these it is necessary to kill the bees and dig out the combs. A further improvement is the use of a box con-

taining wooden frames which can be removed with the combs without tearing the hive apart. But this is far from the simple invention it appears to be. At first such frames were completely ignored by the bees, who simply built their combs criss-cross among the frames, making them entirely worthless. By close observation, a few early beekeepers showed that such frames must be built to very exact measurements if the combs were to be built *in* the frames rather than *across* them. These measurements are closely related to the dimensions of the body of the bee and its reach (Fig. 326). Another great advance consisted in making flat sheets of wax in special presses, upon which were embossed the outlines of the hexagonal comb that the beekeeper desired the bees to build. Again, slight variations from the standard set by the bees make such foundation sheets completely worthless, for the bees simply tear down any structure that differs in form and dimensions from their own instinctively accepted pattern. Nor must any other wax than beeswax be used, for a foreign wax is recognized by the bees and promptly removed from the hive.

The honeybee has in no way been domesticated. It is just as "wild" as it ever was; it is man who has adapted himself to the ways of the bee.

INSECT SOCIAL STRUCTURES

The Bee

Of all insect developments, perhaps the most striking is the evolution of insect societies, which are superficially much like our own though fundamentally quite different. Considering the number of insect species, social organization is a rare phenomenon, for only two groups have evolved it to a high degree, the termites and the hymenopteran wasps, ants, and bees. The former, physically, are more primitive. Perhaps we can best see how this social activity evolved if we begin by tracing it in its simpler forms.

Solitary Bees. There are more than 12,000 species of bees, and almost all of them are solitary and show little indication of a dormant

social trend. Only a few establish communities, though the solitary bee may show remarkable nest-building instincts and may make elaborate provisions for the young, but despite this it remains a solitary creature. *Osmia papaveris*, the poppy bee, is typical. Early in spring, the female emerges from hibernation. She then digs an urn-shaped hole in the ground, lines it with fragments cut from the blossoms of poppies, fills the cavity with pollen, lays a single egg in it, and covers the hole with earth. She then leaves it, and buries other eggs in the same manner. In due time the egg hatches into a larva which feeds and grows upon the stored food, pupates, and develops into an adult bee. The cycle is repeated until hibernation begins again. The mother never has physical contact with its offspring, which are self-sufficient. She does not even see them.

Another solitary bee, the leaf-cutter, *Megachile cetuncularis*, appears to have made a first step toward socialization. This is the insect responsible for the circular holes cut out of rose leaves, so often a source of annoyance to the gardener. This bee uses rose leaves to line its nest, which is tubular and contains a chain of provisioned egg-chambers. This is no community life; but, as we shall see, it may represent a step in that direction.

Simple Bee "Societies." Another step is shown in the bee *Anthophora*, which builds its nests in earth or clay banks or, in the West, in the sun-dried bricks of adobe houses. These bees are gregarious, and many hundreds may

Fig. 325. Colonies of honeybees in old-fashioned skeps. It was the wasteful and cruel custom to kill the bees in these colonies in order to obtain their honey.



nest in the same wall. The nests are tubular, and frequently several bees have nests branching from the same opening. Since their social progress appears to consist only in a certain toleration of each other, such that they may pass or sit side by side without open hostility, it can hardly be said that they have developed communities.

Still another advance is exhibited by some of the more common mining bees of the genus *Halictus*, which also build tunnels in banks and are gregarious. The individual nests of these tiny bees branch off from a communal passageway, which is closed to the "general public" by a sentinel who can close the restricted entrance with his head, which almost fills the opening. Only to a bee that "lives" in that particular string of apartments is the gate opened. Each bee builds a number of nests, all branching from the same corridor, and in this process so much time is consumed that the eggs in the first one hatch, pupate, and emerge as bees before the last cradle is completed. Thus there is contact between "mother and child," as both may exist concurrently; but that is all.

The Bumblebee. Further steps of interest may be learned from the nest-building bumblebees. Only the fertilized females survive the winter. In the spring these first lead the life of a typical solitary bee, finding nests in a sheltered crevice,

where they build one or more large wax cells. These are filled with honey and pollen and then a number of eggs are laid. The cells are periodically reopened by the mother so that she may replenish the food supply which she obtains on further foraging trips. Despite her diligence and care, feeding conditions are apparently not optimal, for some of the larvae die and those that do pupate are smaller than the mother, their ovaries are underdeveloped, and their instinct for mating is replaced by a nursing instinct. They forage, feed the young, build more cells, and in general assume the care previously performed by the mother. Since the mother now devotes herself to egg-laying and rarely leaves the nest, the colony quickly grows. As it prospers, and feeding conditions become optimal, larger females are produced which assume more and more the proportions of the original mother of the colony. These are fertilized by males, which have now also been produced. These, the drones, are quite lacking in instincts other than those for mating, and they soon die. When cold weather again sets in, all members of the temporary community die but the young fertilized females, which hibernate and start new communities the following spring. A long step has been taken here toward a perennial bee community, for the only necessary step remaining is that larger groups with better

Fig. 326. A one-comb observation hive showing the modern manner of inducing bees to build their combs on removable frames. Thus removal of honey causes but little disruption in the hive.



nests be introduced, in order to enable the whole community to live through the winter rather than the female or "queen" alone.

The Honeybee. In the honeybee, the community has in a sense almost become a super-individual, while the single bees have been reduced to a role roughly approximating that of individual cells in the body of a metazoan. The bees within the unit hive no longer appear to act as individuals, but rather as members of a coordinated whole. Under favorable conditions, the hive may be so gentle that one may safely lift out frames with an ungloved hand. The same hive, under unfavorable conditions, may launch a vicious attack on an innocent bystander without apparent motivation. Such an attack is rarely perpetrated by a single bee, but by a whole squadron attacking as a unit. It is a fascinating thing to see — though not to experience.

Within the hive there may be as many as 100,000 bees, most of which are sterile females or workers. There may be a few drones, depending on various conditions, and in the entire great city there is but one fertile female, the queen. Instinct, that inborn, unlearned disposition to act in a certain way, controls the entire mechanism of the state. Whereas winter disrupts the communities of bumblebees, the honeybees have developed a community sufficiently strong to survive the cold season as a unit. Highly interesting in this connection is the fact that the hive-unit generates its own warmth. Even on the coldest winter day, the metabolic activities of the individual bees maintain a temperature of about 10° C (50° F.) within the hive, and there is ceaseless activity as bees from the periphery move in to warm up while others are pushed farther out. Too small a colony — and of course a solitary bee — quickly dies if the temperature approaches the freezing point, for the individual bee has not attained warm-bloodedness.

The queen of the hive has been grossly misnamed. She has no control or dominance over the other bees, but is completely dependent on them. Her sole function is egg production, in which she is indeed phenomenal. A mature

healthy queen may lay 2000 or more eggs in a single day, and she can keep this up for weeks on end during the spring and summer, and for as many as four or five years. In return for this amazing performance, she is relieved of all other duties. She is fed, cleaned, and groomed. The brood is tended by young workers, and all repair work and foraging is performed by other workers. The method is highly specialized and appears to be successful. The colony has become a unit and lives on year after year, although each individual bee may live only a month or two during the active season. If the queen fails because of old age, and no young queen can be provided, then the colony too dies out. Periodically a colony splits and new ones are established.

The reproductive cycle in the honeybee explains the origin of specialization within the colony. Eggs laid by the queen are of two kinds, fertilized and unfertilized at will. The former, of which there are many, develop into females; the latter, of which there are relatively few, into drones. For the first three days all larvae are fed on a food of high nutritive value called *royal jelly*, which is secreted by the workers. Thereafter most female larvae are fed the coarser food of pollen and honey and emerge in twenty-one days as sterile workers. But similar eggs placed in especially large cells continue to receive the royal jelly and hatch in sixteen days as young queens. Thus the same genes produce quite different results in individuals fed the two different diets. If the colony in which the young queen bee has been hatched happens to be queenless at the time, she will leave the hive for exploratory trips when she is about five or six days old. A few days later she flies some hundreds of yards until she meets a group of drones. A number of these follow, and one mates with her, after which the pair usually falls to the ground. The queen then struggles to disengage herself and in the process tears the generative organs out of the male, which dies at once. Upon her return to the hive, the workers remove the emptied male organs from the queen, who now has a store of sperm cells that will last her two to four years or longer.

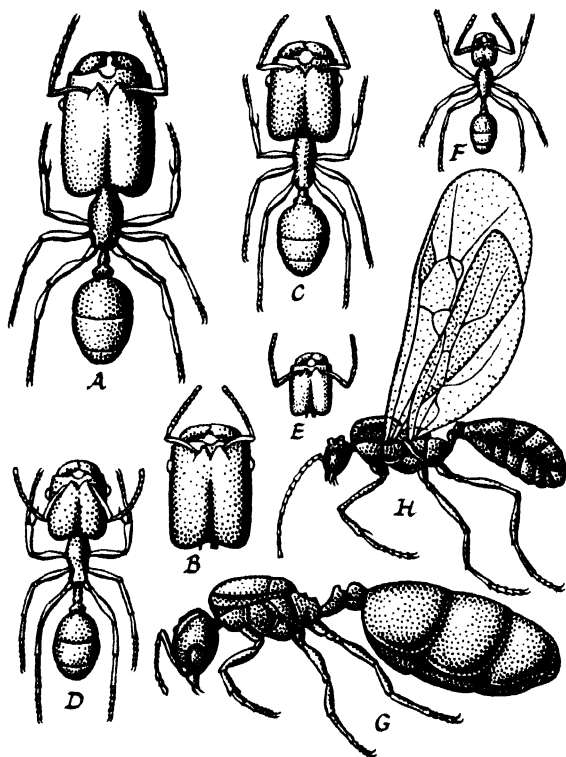


Fig. 327. Polymorphism in the ant *Pheidole instabilis*. A. Soldier. Note enormous head for housing muscles of overdeveloped mandibles. B-E. Intermediate types between soldier and worker. F. Typical worker. G. Dealated female (wings shed). H. Male.

If the colony is prosperous and available space is filled with stored honey, the workers build more queen cells and eventually rear another queen. The instinct of the old queen drives her as a rule, to destroy all such competitors. If the workers are successful in thwarting this instinct, the old queen may assemble some followers and leave the hive, to start a new colony elsewhere. This is called *swarming*, and is one of the most amazing displays of instinct. The old queen flies a short distance and settles on a convenient object, while many of the workers fly in wide circles around her. Gradually these settle down on and about the queen, to form a cluster which may weigh as much as ten pounds. Why some bees leave with the old queen while others stay is not known. It is not a matter of age, for young and old workers are found in both groups. After

hanging in the cluster for some time — usually a few hours, but sometimes for days — the whole mass suddenly rises into the air and appears to head straight for a new home, suggesting to us that there is some system whereby a new home has been previously selected.

Ant Societies

Amazing as we find the social organization of the bee, that of the ant yet surpasses it in many ways. The social behavior of ants seems sometimes like a caricature of human society, with parallels to human achievements and foibles, almost without end. It is now well known that some species of ants devote themselves to agriculture, especially to growing fungus underground. Some varieties keep “cows” in the form of aphids (plant lice), which they tend with as much care as we do our domestic animals. They are plagued with “rats” in their homes, in the form of minute insects — sometimes smaller varieties of ants — that live in burrows within the burrows of larger ants. These pilfer the foodstores of their unwilling hosts and escape their chastisement by slipping into small passageways which their pursuers cannot enter. Ant colonies are known to become debauched, succumbing to sweet secretions or stimulants produced by guests that may be sucking dry the very brood of the host. Ants are known to weave, using their thread-spinning larvae as shuttles which they hold in their mandibles. While they lack the ability to make special tools, they have specialized individuals which serve much the same function. In some species soldier ants have become so specialized that they cannot feed themselves, since their enormous scimitar-like mandibles get in the way (Fig. 327). In others, their very lives depend on the services of slaves, so that the “masters” live as virtually a parasitic minority in colonies of “slave” ants which they have established.

Descriptions of ant character have been given by many observers, and they portray ants as perhaps the most belligerent of all animals. They stand on a perennial footing of war with any foreign animal they meet, even with neigh-

boring ant communities of the same or of different species. Each community attempts to extend its territory, thus creating constant border incidents, and frequently ants of one community attempt to commandeer the supplies of another. Would a report on human beings by an envoy from a distant planet read very differently?

The Arthropoda as a Group

A survey of the arthropods, from *Peripatus* and the centipedes to the highest insect, reveals a number of interesting evolutionary trends. The external skeleton traces back beyond the phylum, and as it becomes more highly specialized, brings several subordinate modifications. The tendency for the higher arthropods to show an increasing difference between larval and adult stages comes at least partly from the presence of this exoskeleton. Since growth is intermittent and can usually occur only when the skeleton is discarded, drastic body changes come about suddenly, though internal preparation for them is made at a prior time. Moreover, selective processes tend to accentuate the differences between larva and adult.

Also in the arthropods the metameric plan has been exploited to its fullest, especially in the appendages. Starting with a form possessing many segmental appendages, there has been a gradual differentiation between these, a specialization of them, in different body regions. In the higher forms, there has occurred a grad-

ual merging of segments of the appendages to produce organ complexes, such as the mouth parts, in which the basic appendage has been changed almost beyond recognition. Fusion of segments has not been restricted to outer structures, but has involved internal systems as well. This is shown by the fusion of ganglia in the nervous system.

As the segments differentiated externally, internal organ systems showed similar differentiation and centralization. The digestive tract developed a series of specialized chambers. Excretory structures changed from the metameric nephridia of annelids to the green glands of the crustaceans and the Malpighian tubules of the insects, concentrated in a single body region.

Finally, the highest representatives of this phylum have acquired complex instinctive reactions and even a limited degree of ability to learn — that is, intelligence. Even the adaptive characteristic of warm-bloodedness, generally attributed only to the highest vertebrates, may be found in incipient form among the colonial bees.

From the standpoint of man, there are fortunate limitations in the fundamental structure of arthropods, for so far as we can tell, exoskeletal structure and tracheal breathing are efficient only in organisms of modest size. This limitation and the relative inflexibility of the arthropod's nervous system may be the determining factors in man's struggle with this largest, most extensive, and most highly evolved of all invertebrate phyla.



Forerunners of the Vertebrates: Echinoderms and Primitive Chordates

Although the mollusks and insects represent the highest developments among the invertebrates, the animals with backbones — including the fishes, amphibians, reptiles, birds, mammals (and man) — have in many ways outdistanced them on their own branch of the phylogenetic tree. Leading toward the vertebrates are two other invertebrate groups, some of whose members are strikingly primitive compared to the highly evolved mollusks, crustaceans, and insects. These are the echinoderms — the starfishes and their relatives — and the pre-vertebrate chordates, unassuming animals without a backbone but with a notochord, an internal rod of cartilage which gives the body a certain firmness and support. The echinoderms are considered to be offshoots of the chordate branch because of certain peculiarities in their embryological development and in their larval stages. The primitive chordates are still closer to the direct ancestral line that led to the vertebrates.

THE STARFISHES AND THEIR RELATIVES

The phylum *Echinodermata* (Gr. *echinos* = hedgehog + *derma* = skin) owes its name to the various forms of spines which grow on their exoskeletons. They are found in all the seas of the world, some near the shore in the zone of the breakers, others in the greatest ocean depths. If the mollusks are perhaps the strangest creatures in the animal kingdom, the echinoderms are powerful contenders for this title. Whereas most other animals, especially the higher ones, have a head and a tail, a left side and a right, there is little evidence of bilateral symmetry in this phylum. The echinoderms

are characterized instead by a five-armed radial symmetry and by their peculiar spinness, and hence even the layman will generally have no difficulty in determining their general relationship. Beyond this general resemblance, however, few characteristics are common to all members of the group. Some swim and some crawl; some are attached to long stalks like spiny flowers; others look like leathery balls or fleshy sausages. Some have no spines. And the five-armed radial pattern of others has been greatly modified by evolutionary changes. Yet with all their diversity, no member of this phylum has ever evolved into a land form.

The echinoderms are as eccentric in their nervous and sensory equipment as in appearance. Although they have no concentration of nerve tissue that could properly be called a brain, many of them are very sensitive and respond swiftly. Among the starfish, all five arms are used as equivalent structures, and little preference is given to any of them, though two are often more closely spaced than the other three. The nervous system extends into each of the arms, as do the digestive and reproductive systems. Poorly equipped with specialized perceptors, these animals yet seem to be generally sensitive to various stimuli. Even in those which have eyes — one at the tip of each arm — the removal of the eyes does not rob the animal of its power to react to light. Since it has neither end nor side, a starfish or sea-urchin may travel in any direction with equal mediocrity. Feet, by the hundreds, are evenly distributed in rows over the ventral surfaces of the arms. And while they appear to wave more or less aimlessly in all directions,

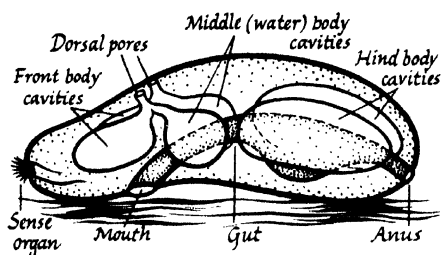


Fig. 328. Simplified diagram of dipleurula larva of echinoderms.

somehow the animal moves positively this way or that. The response to food stimuli is also highly developed. Covering the outer surface are minute pincers (*pedicellariae*) on stalks, which give the appearance of acting independently. Small live creatures or fragments of organic matter cause these to writhe toward the source of the disturbance, and what they touch they grasp in their jaws. In this manner even small fishes may be captured and conveyed, by relay, to the centrally located ventral mouth. Echinoderms show by their behavior that they are capable of learning and can adapt themselves to novel environmental conditions.

Evolution of the Echinoderm Pattern

Present ideas regarding the evolution of the echinoderms are based partly on a study of the larvae of living forms and partly on the

evidence provided by fossils. The larvae of various echinoderms — the *pluteus* larva of the sea-urchin and brittle star, the *bipinnaria* of the starfish, and the *auricularia* of the sea-cucumber — all reveal the same general structure (Fig. 328) and develop from the same *dipleurula* stage. This similarity, and the distinct contrast between them and trochophore larvae of mollusks and annelids, justifies the assumption that they must represent modified forms of an ancient echinoderm ancestor. The beginning of the phylum probably goes back to a worm-like, free-floating larval type of organism like the *dipleurula* (Gr. *dis* = two + diminutive of *pleura* = side), literally meaning "little two sides." It was clearly bilaterally symmetrical and had evolved beyond the primitive radial symmetry of its coelenterate ancestors.

Some mutant forms of this ancestral *dipleurula*, having evolved dermal lime-spicules, seem to have adopted a sedentary mode of life and to have attached themselves to a firm base at a point on their bodies midway between mouth and anus. These gave rise to aberrant forms of echinoderms now extinct, but known as fossils. Others appear to have become sedentary by evolving sucker-like structures at the anterior end, near and to the right of the mouth. There followed a drastic reorganization of the internal organs, so that the mouth eventually came to lie on the upper side, causing the intes-

Fig. 329. Serpent stars, aboral (left) and oral surface.

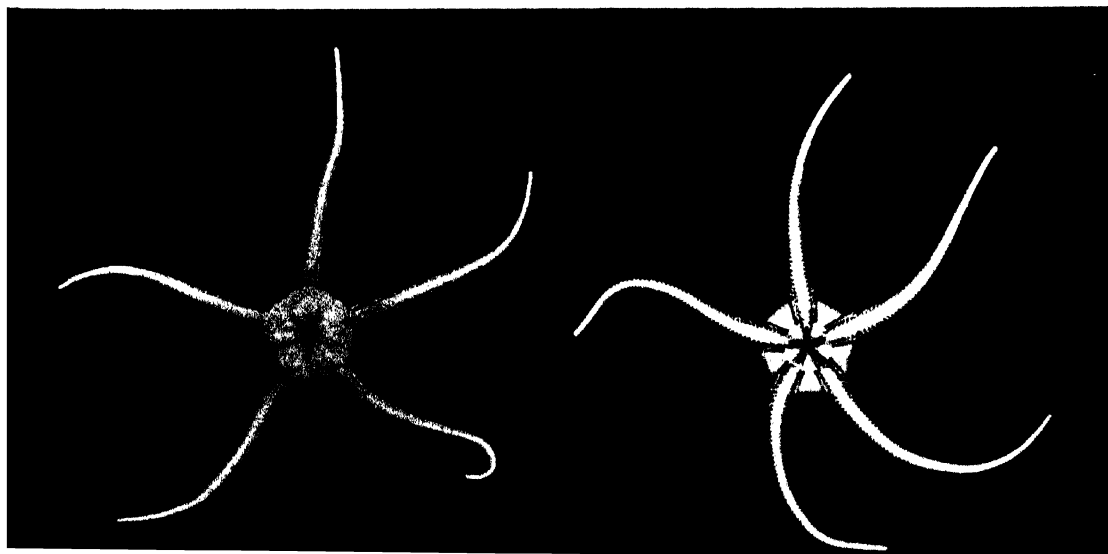




Fig. 330. Sea-lily, a crinoid. Branched arms bear pinnules, small lateral processes, which are arranged on them like feather-barbs. All bear ciliated grooves which together form an extensive food-gathering system.

tine to become loop-like. Ciliated grooves which developed around the mouth served to transport food to the mouth. These changes, by no means hypothetical, can be traced in certain echinoderms of today. The body plan thus evolved was not radial, but became the basis for the radial symmetry which was to be acquired later. Eventually five of these radial ciliated grooves dominated, turned upwards from the cup-like body with the mouth at the center, and gave the animal somewhat the appearance of a lily.

All modern echinoderms trace their ancestry to such sessile, stalked animals. Some still retain this general plan. Others, perhaps as a result of life in the surf zone, became re-adapted to a free-living mode of existence, possibly first by the selection of those which survived after having been broken from their stems. Essentially, the starfishes are remodeled de-stalked echinoderms turned over, so that the mouth-

side is down. In yet a further series of developments, some of these secondarily free-living echinoderms, with radial symmetry acquired during their intervening sessile evolutionary period, came to lie on their sides. They thus evolved once more into worm-like creatures, with a top and a bottom, a head end and a tail end, and the anus once more shifted to the rear. These, in other words, for a second time began the transformation to bilateral symmetry. They are the sea-cucumbers. The aimless shifting back and forth from sessile to free-living habits and from bilateral symmetry to radial symmetry manifested by the echinoderms is evidence enough of the lack of any plan or purpose in evolution beyond the "survival of the fittest."

Types of Echinoderms

There are five modern classes of echinoderms, several others having become extinct. One of the surviving groups is the class *Crinoidea* (Gr. *crinon* = lily). Aptly named sea-lilies because of their appearance, most of these animals are sessile. They are also referred to as feather-stars, a name more appropriate to those which have become free-living. Evolution from sessile forms to those which have lost their stems and crawl about actively can be traced from the Jurassic to the present. Indeed, even today feather-stars, which belong to this class and which are free-living as adults, are stalked when young. The arms bear feathery lateral processes and may be branched. The upper surfaces of arms and pinnules bear ciliated grooves which gather and convey food. The combined length of the ciliary grooves of a single crinoid may exceed a thousand feet (Fig. 330).

The common starfishes belong to the class *Asteroidea* (Gr. *aster* = star + *eidos* = form), though they might more aptly be called "sea stars." The five arms — there are more in some varieties — are not sharply marked off from the main body. Tube-feet with suction disks are located in grooves on the undersides of the arms. While there are over a thousand species of starfishes, they are all much alike.

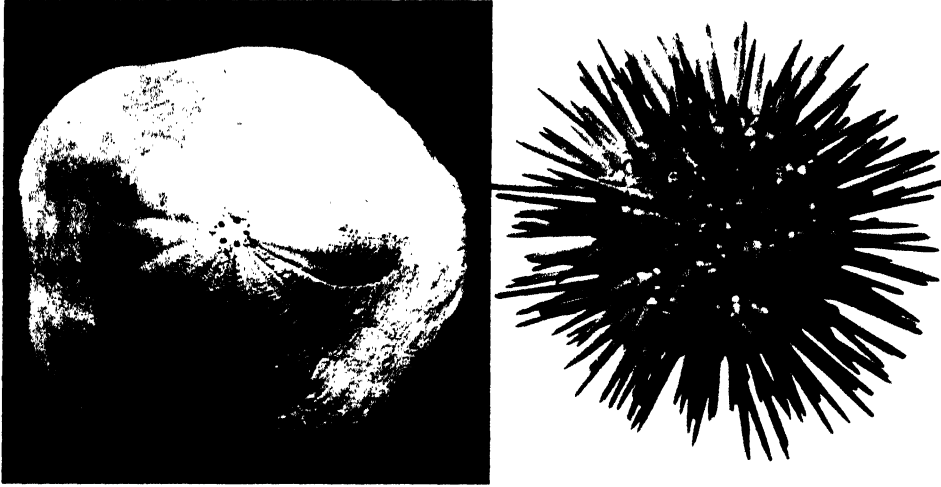


Fig. 331. Sea-urchin. Spines may be short and stout, or long, slender and poisonous. Sand dollars (left) are common on many seashores of the United States.

A second group is the class *Ophiuroidea* (Gr. *ophis* = serpent + *oura* = tail), which includes several varieties. Among them are the brittle stars, remarkable for their ability to slough off members under stress and to regenerate them subsequently. The serpent stars have sinuous, agile arms, and some of the basket stars have repeatedly forked arms with which they attach themselves to corals. In all of these the slender arms are sharply marked off from the disk-like body. The tube-feet have no suction disks, and are not located in grooves (Fig. 329).

The sea-urchins belong to the class *Echinoidea* (Gr. *echinos* = hedgehog) and many do indeed look like rolled-up hedgehogs. Usually globular, they are covered with spines which are movable and may be used as stilt-like feet for walking. The spines vary from slender needles to blunt club-like structures. There are no arms, or rather, these have become fused to form the spherical, box-like skeleton. An odd modification is the disk-like sand-dollar (Fig. 331).

Of still a different form are the members of the class *Holothuroidea* (L. *holothuria* = a water polyp), the sea-cucumbers, so called because of their shape. The long body is

pliable and leathery. Spines are absent, for the skeleton has been reduced to small ossicles embedded in the body wall. Unlike other members of the phylum, these animals lie on their sides and have the mouth at one end and the anus at the other. Thus, not attached, and with their body axis horizontal, some of them have acquired a degree of secondary bilateral symmetry. In China great quantities of them are collected and dried to produce "trepang," which is used as an ingredient in soups (Fig. 332).

Asterias: A Typical Echinoderm

This typical five-rayed asteroid illustrates the general body structure of echinoderms. Perhaps the most striking feature of this pattern is the radial symmetry of each organ system. In perfect accord with the radial arrangement of the arms, the nervous system, digestive system, primitive circulatory system, reproductive system, and the unique water-vascular system are all either centrally located, with radial branches, or are constructed on a ring-pattern, also with radial branches. It is at first not easy to see how such perfect radial symmetry could have evolved from a bilaterally symmetrical original. But a few clues, espe-



Fig. 332. A sea-cucumber showing three of the five rows of tube-feet extended. The tentacles around the mouth are slimy and assist in trapping small animals which are then sucked off by the mouth.

cially the nature of the larval development, indicate that the ancestors really were bilateral. In the adult starfish, too, the position off-center of a sieve-like plate may be cited as an indication of a non-radial origin.

The upper or aboral surface of the starfish is rough and warty (Fig. 333). The skin is covered with hundreds of short, conical spines growing from beneath the epidermal layer. Between the hard, small, bone-like structures that form an endoskeleton shield just under the skin, thin-walled tubes, protrusions of the body cavity that push out into pouches of the skin, project above the surface of the arm. These are skin gills, the only respiratory structures the animal possesses. Because of their numbers, they enormously increase the surface available for gas exchange. But the great sensitivity of many starfishes to a depletion of oxygen in the water suggests that the skin gills do not greatly exceed the minimum need of the animal for respiratory surface. Also on the surface are the pincer-like pedicellariae, which function in protecting and cleansing the skin. To one side of the center, near the junction of two arms, there lies a clearly defined circular area consisting of a perforated plate, the sieve plate, which serves as an intake for water used in the unique water-vascular system of the echinoderms. The anus is located at the exact center point.

The under surface of the starfish, which is its *oral* side, presents a much livelier and more interesting view. Hundreds of tiny feet wave

at us. An arm twists with evident purpose until some of the tube-feet come into contact with the ground, and when these are again firmly anchored, it takes but a few seconds for the starfish to turn itself over into normal position again. To continue examining the oral surface of a living starfish requires repeated turning over, for the animal is persistent in regaining its accustomed position. The mouth is easy to locate, in the exact center of the star. Along the axis of each arm is an *ambulacral groove* in which the rows of tube-feet, each one ending in a small suction cup, are arrayed. Especially long spines, inclined inward from the margins of the grooves, protect the tube-feet and the nerve cord, which runs along the bottom of each groove. It is in this view that the peculiarly decentralized structure of an echinoderm strikes us most forcefully, and our eyes unconsciously wander from point to point looking for a directing center or brain, but we can find none. The nearest thing to it is a series of four more or less concentric rings surrounding the mouth, with spokes radiating into the arms.

Structures and Functions

To watch a starfish open an oyster or a clam is a real experience (Fig. 334). It slowly wraps itself around the hapless bivalve, attaches its cup feet to both shells, and pulls until the closing muscles of the mollusk are exhausted and the shells open. The starfish then everts the lower part of its stomach over the body of the shellfish and secretes enzymes which be-

gin their digestive action on the soft tissues. These can then be sucked into the stomach for further digestion. From the stomach food passes into the pyloric sac, which has five pockets, each with richly branched tubes leading into the arms (Fig. 335). Here digestive enzymes are produced and food is further digested and absorbed. The little indigestible material passes into a short rectum. In some species there is no anus and the digestive tube ends in a blind sac.

Several sets of ring-like structures, with spokes radiating into the arms, surround the mouth. The most important are the *ring canal* of the water-vascular system and the *nerve ring*.

The water-vascular system of the echinoderms, found in no other animal group, assists in the combined functions of respiration, walking, and feeding. The ring canal of this system is quite symmetrical except for the stone canal, which runs to it from the sieve plate (Fig. 336). Water entering the sieve plate circulates through the system to small bulbs, the *ampullae*, on the oral surface. Muscles surrounding these force the water into the tube-feet, much as the rubber bulb on the end of a medicine dropper forces water out of the tube when the bulb is squeezed. Since the feet are closed at the ends, the internal pressure of the water extends them, and muscles in their walls control the direction of their extension. Moreover,



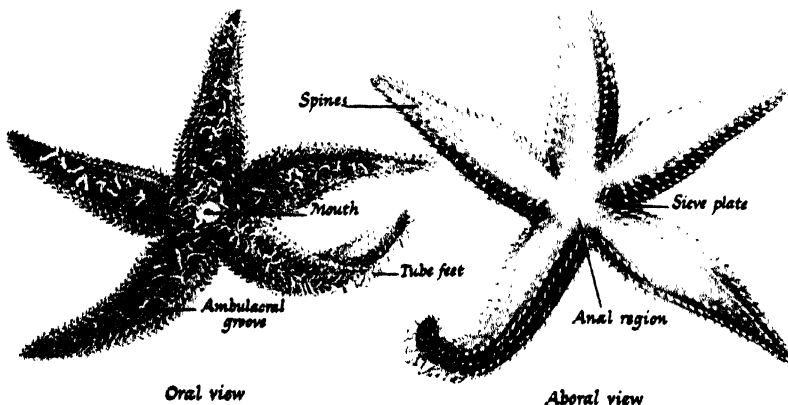
Fig. 334. Starfish about to eat a mussel. Continued tension will exhaust the closing muscles of the bivalve so that the shells will open.

the feet are equipped with suction cups so that when they press against a solid surface and the internal water pressure drops, they adhere firmly. Longitudinal muscles then shorten the foot and haul the starfish in the direction in which the tube-feet are anchored.

The blood-vascular system is poorly developed in the starfish as in other echinoderms. There is a vascular ring and radial canals; but there is no heart, and there is no blood distinct from the general coelomic fluid. Amoeboid cells in the coelom and ring systems appear to assist in the distribution of food and the collection and disposal of wastes.

Finally, the nerve ring immediately sur-

Fig. 333. Oral and aboral surfaces of starfish (*Asterias vulgaris*).



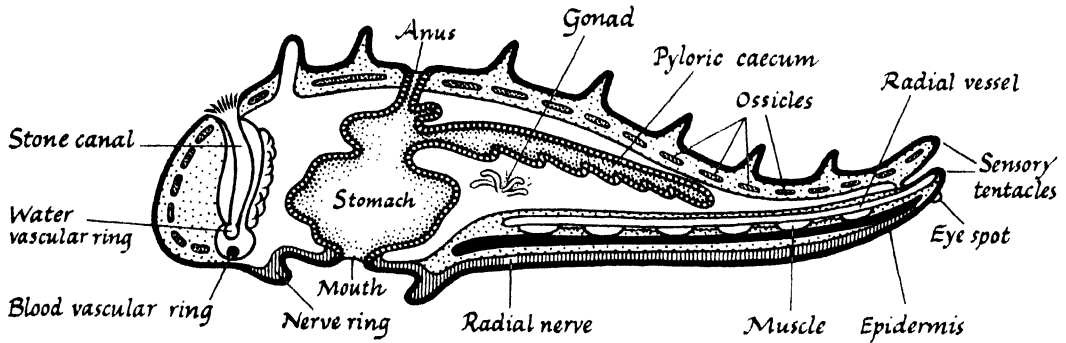


Fig. 335. Longitudinal section through the disk and arm of a starfish.

rounding the mouth opening extends radial branches into each arm, and these in some species terminate at the end of the arm in a pink eye spot. An anal nerve ring gives off branches to the epidermis. There are no clearly marked ganglia, and no concentration of nerve tissue which could be called a brain. Yet, despite the lack of centralization in the nervous system, clearly a case of retrogressive development, the starfish is remarkably sensitive to stimuli. Some of its reactions appear to occur independently of the nervous system, though the latter is considered to perform certain generally directive functions. The pedicellariae act as independently as though they were symbiotic animals and not organic parts of the main body. When stimulated, they respond by grasping and making movements designed to remove the source of stimulation. Because of this, they may even become embroiled with the pedicellariae on another arm of the same animal!

Reproduction

Most echinoderms reproduce sexually, and the sexes usually are separate. In both sexes, there are five pairs of gonads, one pair in each arm. Sperm and eggs are discharged into the water through pores in the angles between the arms. There the fertilization of the egg occurs if a sperm cell finds it. The eggs are small and are produced in great numbers. When fertilized, an egg hatches into a *bipinnaria*, a free-floating larva which is self-sufficient and which

eventually transforms into the young starfish. This free-living larval stage may be considered not only as a recapitulation of a distant ancestral form, but as a mode of adaptation for the dispersal of organisms which are not equipped as adults for extensive travelling.

Certain other starfishes, as well as other echinoderms restricted to limited regions, have evolved what is known as brood protection. In such cases fertilization may be internal or external, depending on the nature of brood care. Generally the relatively large, yolk-rich eggs are produced in small numbers — dozens or hundreds, whereas echinoderms that do not practice brood-care produce thousands. In some species the eggs are retained in the enlarged oviducts or in other modified structures which serve as brood pouches. In other species the eggs are laid and then are stored in safe places in pockets between the spines or in other pouches. Here the eggs undergo complete development and hatch as echinoderms already in adult form, having passed through their modified larval stages prior to hatching. Brood-care of this sort is limited to protection of the young against enemies — the mother does not contribute toward their feeding, beyond the yolk originally stored in each egg.

Eggs of starfishes and sea-urchins have been used extensively for experimental work in biology, especially because of their availability, their uniformity, and the ease with which they can be cultured. The fact that they may be induced to develop parthenogenetically by

changing the chemical composition of the sea water, by pricking with a pin, or by electrical stimulation, has yielded insight regarding the potentialities of egg and sperm nuclei and the role of the cytoplasm in determining the future organism.

Regeneration

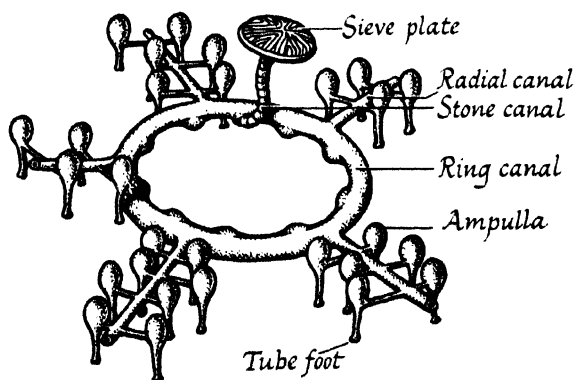
Echinoderms, and starfishes especially, are capable of astonishing feats of regeneration. An arm broken from an *Asterias* is regenerated with ease. Yet more remarkable is the fact that the detached arm may also regenerate an entire body and four new arms, thus producing an entire new starfish. In some starfishes this regenerative power becomes an asexual mode of reproduction by budding and supplements the sexual method. The simple radial anatomy of *Asterias* makes this ability less difficult to understand than it would be for an arthropod; for each arm of a starfish contains an equal share of the anatomical structure of the entire animal. Regeneration is primarily a proliferation of tissues already there.

Chordate Affinities

Superficially, echinoderms give little evidence of being related to the chordates, and we may ask why they are included in the chordate line of evolution. Certainly they give little or no indication of the segmental plan of the chordates, or of their typical gill slits, or of the stiffening rod, the notochord, after which the chordates have been named. Primarily the evidence rests upon similarities of larval structure and embryonic development in the two groups. Both groups have a coelom or body cavity — but so have the arthropods and many others. However, the coelom in both chordates and echinoderms arises embryologically in a similar and unique manner. In both chordates and echinoderms it develops from hollow mesodermal pouches, and not, as in arthropods, by the formation of cavities in a continuous band of mesodermal cells. Furthermore, the original mesodermal tissue in the chordate line arises from lateral pouches of the primitive endoderm,

while in the main phyla of the other great phylogenetic branch of the animal kingdom, that of annelids and arthropods, the mesoderm arises from cells simply produced adjacent to the primitive endoderm. Finally, echinoderm larvae, which, as we have seen, are all quite similar to each other, are also similar to the free-swimming larvae of certain primitive chordates, such as the acorn worm *Balanoglossus*. To be sure, similarity of structure does not always imply close relationship. It is often the result of prolonged subjection to similar environmental conditions. It is also true that larvae, though they may have preserved certain primitive characteristics, are frequently themselves altered by adaptive evolution. But the frequent presence of the structurally quite different trochophore larva of annelids and arthropods in the very same environment as the larvae of the echinoderms shows that common environment need not cause convergence. The structural similarity of echinoderm to chordate larvae suggests, then, that these two groups did spring from a common ancestral stock and from the same branch of the animal family tree. Segmentation in the chordates was apparently acquired after their ancestors branched off from those of the echinoderms. If this was so, the segmentation in our own branch appears to have come about by a parallel but distinct evolutionary development from that which produced the segmentation of annelids and arthropods. That is why the starfishes, the sea-cucumbers, and their near relations are thought to be so much closer to the direct line of vertebrate

Fig. 336. Water-vascular system of starfish (diagrammatic).



(and human) evolution than are the much more highly developed mollusks and insects. The echinoderms have specialized and then retrogressed.

THE PRE-VERTEBRATE CHORDATES

The *Chordata* (L. *chordatus* = having a cord) compose the last great animal phylum to be considered, and the one most important to us because it includes man and all those animals upon which he most depends. The lowest and simplest members of this phylum, however, show little resemblance to those animals which represent the climax of its evolution — the vertebrates, and particularly the mammals. Though little known by the average person, these primitive chordates are biologically of great interest because they show us so much about the possible beginnings of the dominant vertebrate pattern.

Despite great differences in size and form, all chordates have in common certain basic characteristics. At first glance these features may not appear either momentous or revolutionary, but they are basic, and they are exclusive to this group.

1. All chordates have, at one time or another, a stiff elastic dorsal rod which runs part or all the length of the body. This is the *notochord* (Gr. *noton* = back, + *chorde* = cord). In the lower chordates, unless lost by retrogressive evolution, it is present throughout life. In the higher chordates, it is present only during embryonic stages and is soon replaced by the backbone or *vertebral column*.

2. In primitive chordates, up to and including some of the lower vertebrates, a series of paired pharyngeal slits, the *gill slits*, serve for respiration. In higher members of the phylum, gill slits or traces of them appear only during embryonic life and never function for respiration.

3. The nervous system is centralized and derives from a dorsal neural tube. This is produced by the in-rolling of an elongated ectodermal plate (see Fig. 343). The dorsal position of the neural tube, which may later become thickened to form a nerve cord, contrasts

with the ventral position of the nerve cord in arthropods.

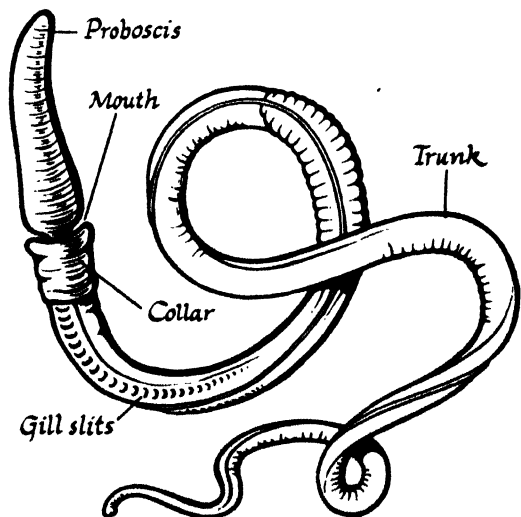
4. Also characteristic of the chordates generally, but especially of the vertebrates, is metameric segmentation. This is by no means exclusive to them, however, for we have seen it well developed in the annelids and more especially in the arthropods.

Of the 70,000 species of chordates, an overwhelming majority are vertebrates — back-boned animals in which the embryonic notochord has been replaced by an articulated column of vertebrae, the spinal column. Included in this subphylum are the fishes, amphibians, reptiles, birds, and mammals, the latter including, of course, man. But among the chordates are also three small and primitive *pre-vertebrate* subphyla, composed of little-known and unobtrusive creatures of no economic importance but of considerable interest to us because of their phylogenetic relationships — to echinoderms on the one hand, shown through larval resemblances, and to the vertebrates on the other, evident from the presence of a notochord.

Hemichordates: The "Half Cords"

The simplest of these three groups is the subphylum *Hemichordata* (Gr. *hemi* = half + *chorde* = cord), so called because a structure

Fig. 337. *Balanoglossus*, the acorn worm, a hemichordate.



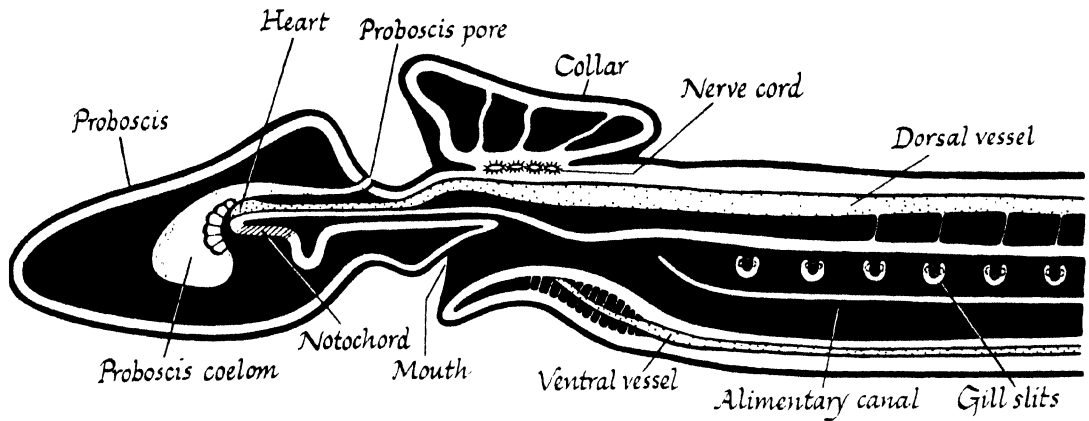


Fig. 338. Diagrammatic sagittal section through the anterior portion of *Balanoglossus*.

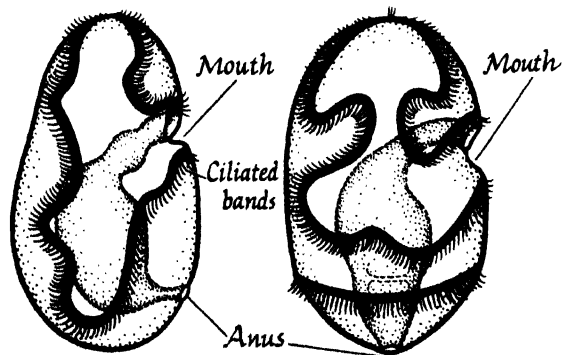
interpreted as a primitive notochord runs along a small portion of the animal's length. Like worms, these obscure creatures burrow in the mud, and they were indeed not so long ago classed as worms. Now their anatomy and the nature of their development make it seem probable that they are an extremely primitive offshoot of the stock that branched off from the echinoderm line and led to the other chordates.

The "acorn worm," *Balanoglossus* (Fig. 337), shows the principal evidence for the theory of the chordate relationship of this group. In this small creature the tubular alimentary tract, directly behind the mouth, is lined on either side with pairs of gill slits, organs found otherwise only in chordates. Anterior to the mouth is a swollen structure, the proboscis or head, specially adapted for burrowing through sand. Within the proboscis an outgrowth of the digestive tract has been interpreted as a notochord, and this may be a permissible interpretation, since the notochord of other animals, more obviously chordate, arises in a similar manner. The nervous system of *Balanoglossus* is diffuse, but there is some dorsal concentration of it, since it forms a tubular structure in the region of the collar; and a dorsal neural tube is an exclusive characteristic of chordates. In addition to the dorsal nerve cord, however, *Balanoglossus* also has a ventral one. Segmentation is primitive but clearly apparent throughout the

organism. These, then, are the features upon which rests the claim that *Balanoglossus* is a primitive chordate. In general, these same characteristics are found in the other hemichordates.

The *tornaria* larva of the hemichordates constitutes a clue of intense interest, for it so closely resembles a typical echinoderm larva that its discoverer, Johannes Müller, mistook it for one (Fig. 339). This is strong evidence of a relationship between the hemichordates and the echinoderms. Hence if, as seems likely, the hemichordates are really chordates, the *tornaria* larva establishes a bond between the entire phylum Chordata and the starfish clan.

Fig. 339. Larva of typical echinoderm at left and *tornaria* larva of acorn worm, a primitive chordate, show striking resemblances in general structure, cilia, and digestive tract.

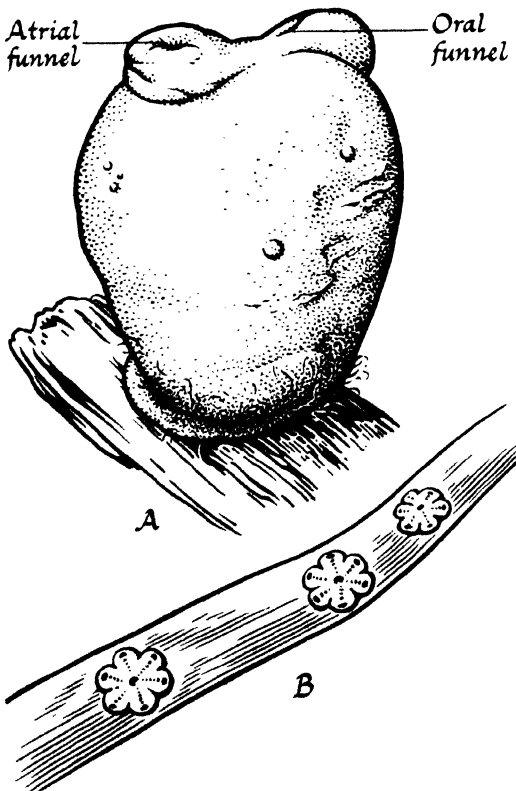


Urochordates: The "Tail-Cords"

Another group with only a trace of a notochord is the subphylum *Urochordata* (Gr. *oura* = tail + *chorde* = cord), in which the notochord appears only in the tail of the larva. Also called tunicates because of their tunic or mantle-like body covering, these animals are commonly known as sea-squirts, since they abruptly contract and squirt water out of their body openings when they are irritated (Fig. 340).

Until quite recently the tunicates were thought to be a branch of the mollusks, because of their strikingly similar siphon arrangement. Indeed, the mature tunicate reveals little that would suggest a chordate except for its perforated pharynx with numerous gill slits. But the tunicate larva has all three exclusive chordate structures: the dorsal hollow nerve cord, the notochord, and the pharyngeal gill slits.

Fig. 340. Two Urochordates (tunicates). A. *Pyura aurantium*, a single sessile tunicate. B. *Botryllus magnus*, a colonial tunicate, growing on eelgrass.



The simple heart is ventral and somewhat anterior to the stomach, as in many higher chordates. By fortuitous mutations and by uncompromising selection of those that were favorable, man might have evolved from such an unpromising beginning — indeed, he probably did. For the tunicate itself, the course of development was radically different. A mutation, or a series of mutations, which led to the development of adhesive papillae at the anterior end of the ancestral tunicate apparently established it as a sessile animal and gave it an adequate way of life with a minimum of effort, or perhaps of danger. This was no doubt only one of many possible patterns for survival. In a sessile creature there is little need for a highly developed nervous system or for specialized organs of perception, and in accordance with the general rule that unneeded structures disappear, the tunicate has largely lost them. Thus in the adult, the eyes possessed by the larva disappear, together with most of the central nervous system. With the abandonment of locomotion the tail, together with its enclosed notochord, becomes useless, and also disappears. A digestive tract within protective mantle folds — a device for circulating water for food and respiratory purposes; a primitive circulatory system with a heart that pumps blood first one way, and then reverses its flow — these are the essential features of the adult tunicate. The step from larva to adult represents marked retrogression and degeneration, despite the specialization for a specific form of life which the animal has achieved. Nevertheless, there is no mistaking its place among the chordates on the evolutionary ladder.

Cephalochordates: The "Head-Cords"

The third and "highest" pre-vertebrate group is the subphylum *Cephalochordata* (Gr. *kephale* = head + *chorde* = cord) — somewhat ineptly named, since the cord extends from head to tail. These creatures are fish-like in appearance, and their structure leaves no doubt of their evolutionary niche. They are segmented and have a notochord throughout life. There are only about twenty-eight species

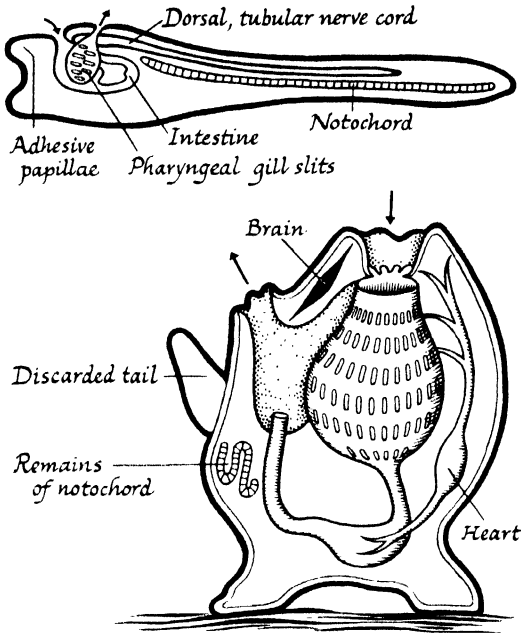


Fig. 341. Larva (above) and adult of a hemichordate or tunicate, not drawn to same scale. Note degeneration of notochord and nerve cord in adult form.

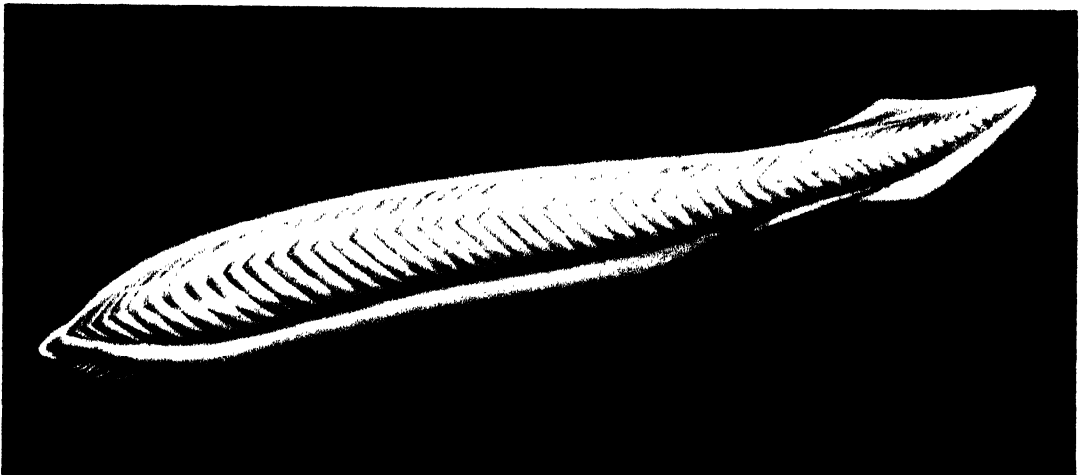
in this small and very uniform group, yet they are found in limited zones all over the world.

A good representative of the group is *Amphioxus* (Gr. *amphi* = both + *oxys* = pointed). Popularly called the lancet-fish, it is not actually a fish, for fish are vertebrates; but it super-

ficially resembles one (Fig. 342), though it has no distinct head and no lateral fins such as true fish have. *Amphioxus* has a dorsal fin that runs the length of the body, and a tail fin. The animal favors shallow, warm, salt-water lagoons with sandy bottoms. Here it spends most of the time buried in the sand while lying on its side, with only its fringed mouth protruding. Water pumped into its alimentary tract and filtered through its gill slits deposits suspended organisms on a sticky secretion, and this passes into the intestine for digestion. A brief sketch of the embryonic development of this basic chordate will help us to understand its structure.

Embryonic Development. In the fertilized egg of *Amphioxus*, two vertical cleavages and one horizontal produce an eight-celled stage. Immediately subsequent divisions result in a hollow blastula with an inner cavity, known as the *blastocoel*. A larger concentration of yolk at one end of the egg has the effect of retarding the rate of cleavage there, so that larger cells result at this, the *vegetative pole*. The cells here soon fold in to produce the inner lining of the gastrula, the inner cavity of which opens outward through what is known as the *blastopore*. The embryo is now a double-walled cup similar to the basic structure of a coelenterate. The outer cells are ectoderm, the inner ones endoderm. The surface of the gastrula is somewhat

Fig. 342. *Amphioxus*, a pre-vertebrate which looks like a vertebrate.



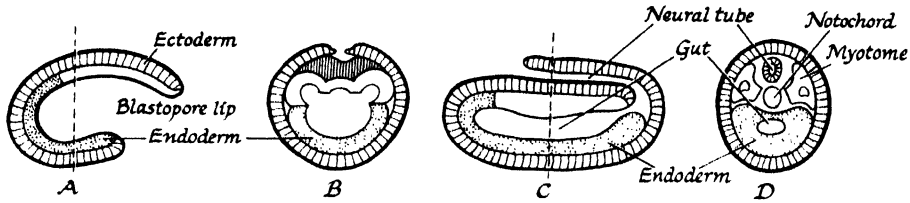


Fig. 343. Diagrams showing the relations of the notochord and mesoderm in *Amphioxus*. *a, c*, longitudinal sections; *b, d*, transverse sections through the planes indicated on *a* and *c*, respectively.

flattened on one side, and this flattened area becomes the *neural plate*. In this there soon forms a groove. The ridges that border the groove on each side increase in height and fold over it until they meet, thus forming a hollow tube, the primitive neural tube.

Meanwhile the gastrula has become elongated, especially through the proliferation of the cells about the lip of the blastopore. Since the cells proliferated here arise from both the outer and the inner cell layers, they have a different origin than those originally invaginated or folded in. It is these cells which soon give rise to the notochord and the mesoderm. The notochord (Fig. 343) arises from the cells that form the roof of the inner cavity and is produced by involution, that is, a turning in, of the cells of the blastopore lip. To the sides, coelomic pouches form from the endoderm and are finally pinched off, thus forming primitive somites or segments. The cavities within these somites merge to produce the coelom or body cavity. Proliferation of the mesodermal tissue pushes it into intimate contact with both ectoderm and endoderm, forming a *somatic* layer of mesoderm on the outside and a *splanchnic* layer on the inside. The mesodermal tissue adjacent to the notochord thickens and eventually produces muscular tissue. Thus the muscles of *Amphioxus*, and indeed of all higher chordates including the vertebrates, are first patterned in somites or sections, in a manner similar to the “meat” sections of a boiled fish.

At this stage the typical and characteristic chordate pattern can be discerned, though we will recognize it more clearly when we study the more familiar structures of the vertebrates.

From this stage onward specialized struc-

tures begin to appear. In *Amphioxus* two lateral folds appear, forming around the body a sort of mantle which opens to the outside some distance anterior to the anal opening. The cavity thus formed is the *atrium* and its posterior opening is the *atriopore* (Fig. 344). The mature *Amphioxus* shows a good many specialized differences from higher chordates. It is in its early developmental stages that it shows the basic relationship clearly.

Structure of *Amphioxus*

Digestive System. When *Amphioxus* is not buried, it lies on its side on the sand, somewhat like a flounder, in a position which accounts for certain of its asymmetries. Food particles taken into the mouth are caught in four longitudinal grooves, the bottom of the pharynx, while the water passes out through the hundred or more gill slits into the atrium and so out through the atriopore. The grooves of the pharynx are equipped with cilia and slime glands, and convey food particles to the intestine. Food is digested by enzymes poured into the intestine from the liver, and is absorbed into the blood stream.

While there is no chambered heart, there is a fairly complex circulatory system. Blood is pumped by a tubular ventral aorta forward through many branched arteries into the capillary network around the gills, thence back through the dorsal aorta and its branches to muscles and organs and forward again toward the liver. The vessel entering the liver, known as the *hepatic portal vein*, corresponds to the hepatic portal system characteristic of the vertebrates. Another vein returns the

blood from the liver to the aorta and thus completes the cycle. Note that blood flows from front to back in a dorsal aorta, whereas in the earthworm it flows the opposite way. This fact supports the view that the vertebrate and annelid circulatory systems arose independently (Figs. 268, 378, and 379).

Excretion is through nephridia similar to those of the earthworm, and respiration is through gills constantly bathed in water which enters the mouth and goes out through the atrium.

Amphioxus is well endowed with segmental muscles, but their primitive nature is shown in their uniformity and lack of specialization. Their action is correspondingly simple, but permits whipping motions which propel the animal through the water or let it burrow head first into the sand.

The central nervous system is feebly developed. There is no brain, but the nervous system is dorsal and tubular, as in vertebrates. Its organs of perception are equally primitive. There are simple sensory cells in the skin and around the mouth, and pigmented eye spots thought to be sensitive to light. An especially large eye spot is located at the anterior end of the nerve cord, and smaller ones are distributed along the cord. Hundreds of tons of these creatures are taken from the mouths of Chinese rivers annually to be used as food.

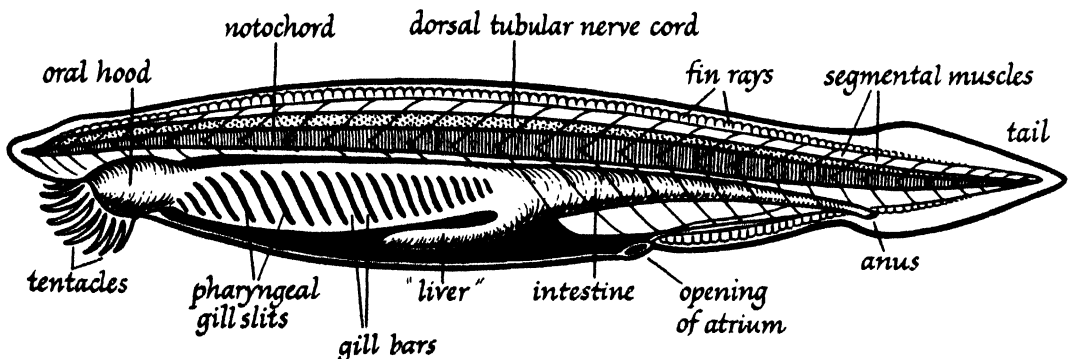
Reproduction. Reproduction is sexual and the sexes are separate. Two dozen or more pairs of gonads — the number differing in dif-

ferent species — are located inside the lateral folds. When the germ cells have ripened, the gonads rupture and release them into the atrium, to be discharged through the atriopore. Once in the water, eggs and sperms shift for themselves, and chance directs their meeting. The fertilized egg undergoes cleavage (see page 381), and when the embryo has five segments, it breaks out of its embryonic membrane and begins its free-swimming life in the ocean. It gradually increases in length by adding additional segments and without metamorphosis eventually becomes an adult.

Summary

In the form and pattern of these primitive chordates, and especially in the course of their individual development, we read the signs of their still more primitive ancestry. Similarly, here we see foreshadowed the possibilities which have been realized in their descendants, the vertebrates. In a rudimentary manner we can see in *Balanoglossus* the simple outline of the body pattern of *Amphioxus*, and *Amphioxus* in turn shows us more clearly the pattern of the vertebrates, even to ourselves. Observing the degenerate adult tunicates, we are made aware of the fact that continued progressive evolution of individual species is not inevitable, but that retrogressions may and do occur, beginning perhaps in what at first appear to be insignificant changes. In comparing *Amphioxus* with the higher vertebrates of today, we

Fig. 344. Sagittal section of *Amphioxus lanceolatus*, a cephalochordate.



are struck by the enormous developments that have come out of so primitive a pattern, while a study of the steps between makes it appear the simplest and most natural process. When we consider the vast difference in extent of environmental control and adaptability between

Amphioxus and man — the latter still built on the basic pattern of the former despite all refinements — we cannot help wondering how another five hundred million years may change the pattern of man, too, should he survive so long.

PART SIX

THE VERTEBRATES





The most highly evolved vertebrates are the mammals, and supreme among these are the primates, including the monkeys, apes, and man. This wistful fellow is Mycetes, the howler monkey, who here belies his name — but see page 491.

The Vertebrate Pattern: Framework and Coordination

The advent of the vertebrates began a new chapter in the history of life upon the earth. The unknown and doubtless inauspicious beginnings of this great subphylum could hardly have given an inkling of its future size and complexity. For the animal life that claims our main attention is almost wholly vertebrate, and the world would be desolate without it. Birds, all furred creatures, the scaly creatures of the land, frogs, toads, and all the fishes of the sea are vertebrates. Only the insects exceed this great group in prominence. No one could have guessed, in the beginning, what an amazing evolution of mental faculties was to set the vertebrates, and especially man, apart from all other animal forms.

The Vertebrate Animal

Vertebrates show a bewildering capacity for adaptability in form and size. They range from such extremes as the mole to the eagle, the mouse to the elephant, the porpoise to the antelope, and from the smallest vertebrate, the mosquito fish, to the largest, the whale. Yet all of them have a basic structure which differentiates them sharply from all other creatures.

The characteristic features of the vertebrates, some of which they share with the lower chordates, are (1) an internal skeleton (endoskeleton) of cartilage or bone; (2) a vertebral column made up of individual structures called vertebrae, replacing the notochord of lower chordates; (3) generally two pairs of appendages, either limbs or fins; (4) a ventrally located heart with two or more chambers; (5) a closed circulatory system and red blood cells containing hemoglobin; (6) a dorsal hollow nerve cord with

the anterior end expanded to form a five-part brain; (7) a more or less distinct head equipped with specialized sense organs; (8) a large coelom containing the essential organ systems; (9) a posterior prolongation of the vertebral column, forming a tail.

The body is generally spindle-shaped and is typically divided into three main regions, head, trunk, and tail. Head and trunk may be separated by a neck, and the tail may be absent. The relative position of the paired appendages varies considerably and one or both pairs, anterior or posterior, may be absent. Or they may be modified for a great variety of functions — running, climbing, flying, grasping, or swimming.

Types of Vertebrates

The vertebrates fall into seven main classes, so sharply divided that they must be considered not as successive stages in evolution but as independent offshoots from a common stem. The lowliest among them are the *cyclostomes*, primitive and degenerate creatures, such as the lamprey, with eel-like bodies, round jawless mouths, and no paired appendages (Fig. 345). Then come the *elasmobranchs*, including the sharks and rays, with jaws and teeth, and in accord with the predacious life thus made possible, streamlined bodies and paired appendages. The elasmobranch skeleton is cartilaginous — probably a degenerate feature. There are gills opening to the outside, and the body is covered with a special sort of scale. Among them are the man-eating shark, the spiny dogfish, and the skates. The third group includes the remaining modern *fishes*, which have bony

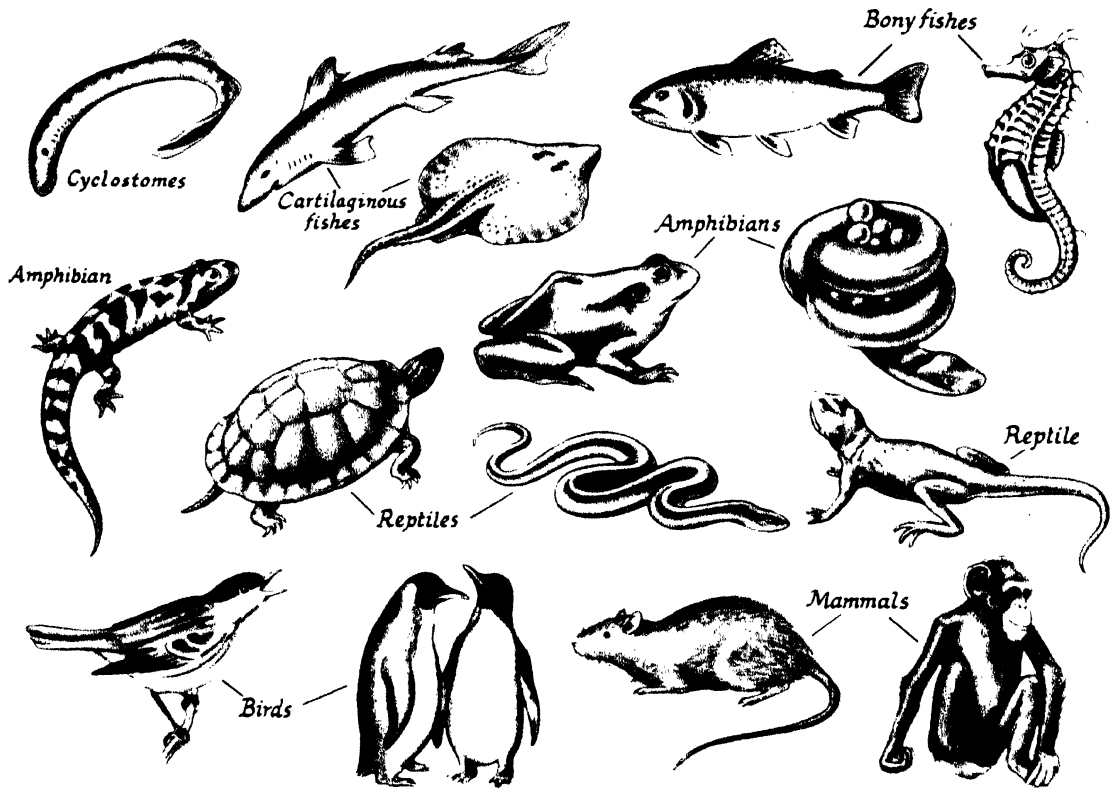


Fig. 345. Representatives of the seven main classes of vertebrates.

skeletons, gills covered by a fold of skin, and scales developing from the skin. Next are the *amphibians*, represented by frogs and salamanders, creatures living part of their lives in water and part on land, and thus usually having gills while larvae and lungs when adult. The first group of completely land-dwelling vertebrates is that of the *reptiles* — turtles, lizards, snakes, and alligators. The sixth vertebrate class is that of the *birds*, warm-blooded, feathered creatures with a controlled body temperature; and the seventh is that of the *mammals*, which in addition to being warm-blooded and protected by a covering of hair, bear their young alive and nourish them with a secretion of their bodies — milk.

The Vertebrate Habitus

Like variations on a basic theme, the vertebrate pattern takes shapes and forms that sometimes all but obscure the fundamental design.

But whatever the modification, the same metameric vertebral column, the same hollow nerve cord with its head-swelling, and the same body divisions, and usually appendages, are all there, however adapted to the demands of a particular environment. Indeed, the pattern has shown itself adaptive to a wider range of conditions than any other, excepting possibly that of the insects — in the water, in the air, and on land, from swamp to desert and from equator to pole. This adaptiveness shows itself strikingly even within single environments.

Thus in the ocean, vertebrates that are free-swimming are generally spindle-shaped, streamlined for rapid motion and maneuvering through the water. Those that dwell on the bottom tend to be flattened, sometimes dorso-ventrally, sometimes laterally. The flounder, originally flattened laterally, has become adapted secondarily to life on the ocean floor by flopping over on its left side. In the course of its de-

velopment from an ordinary young fish into an adult flatfish, a remarkable twisting of its head and body takes place, so that the left eye gradually moves to the right side of the body where it is of use, while the mouth and the pectoral fins become similarly reoriented, the fish's individual life thus demonstrating its ancestral history. Other fishes, like the sea-robin, or gurnard, have become flattened dorso-ventrally, and three free rays of the pectoral fins have developed into supports like legs, on which the fish walks about on the ocean floor. The flying fish uses these same appendages, greatly expanded, as planes and can sail hundreds of feet through the air. Thus in a single vertebrate class within a single environment, the fundamental body plan has been variously adapted to the environmental needs.

This flexibility is even more striking when we consider the diversity of habitus beyond the limits of a single class, though our familiarity with differences in form too frequently blinds us. Although we know that the flying eagle, the deep-sea fish, the burrowing mole, and the climbing monkey are all vertebrates, we tend to forget that there is a vastly greater structural similarity between eagle and fish than between eagle and dragonfly, or between mole and whale than between the mole and the burrowing beetle beside it.

Differences in size do not greatly alter the basic pattern. In mouse and elephant the plan of the nervous, skeletal, muscular, digestive, and other systems is the same. Anyone familiar with the anatomy of a mouse can easily grasp that of an elephant. The differences are the relatively minor ones demanded by specialization in manner of living and in size. The elephant's trunk is still a nose, and his tusks are still teeth. Bone for bone, the skeleton of one corresponds to that of the other.

Vertebrate Structure and Function

The vertebrate plan is that of all the larger animals (except the squids and octopods), including most domestic ones. The entire vertebrate organism, like all the previously studied higher metazoans, consists of a coordinated

group of special systems:

1. The framework: the skeletal system.
2. The driving mechanism: the muscular system.
3. The mechanism of perception and coordination: the sense organs, the nervous system, and the endocrine system.
4. The integument: the skin and its derivatives.
5. The mechanism of distribution: the circulatory system.
6. The food-processing system: the digestive system.
7. The mechanism of gas exchange: the respiratory system.
8. The water-balance and metabolic waste disposal system: the excretory system.
9. The mechanism of propagation: the reproductive system.

Together these form the whole vertebrate, of whatever kind it may be. In general these systems always serve the same functions, and most modifications in them are merely changes in degree — adaptations to specialized modes of life, rather than basic changes in function.

But as we move from the lower vertebrates to the higher, we see a fascinating complex of modifications in these systems, adaptations to varying environments and modes of life, and the story of these developments is a large part of the history of vertebrate evolution. In this chapter and the next we shall trace the chief of these adaptations and developments.

THE SKELETAL FRAMEWORK

Advantages of the Internal Skeleton

The internal framework of the vertebrates gives them one advantage possessed by no other animals: size. It is not mere chance that all large land animals, and most large seaw dwellers, are vertebrates. Except in very small organisms, a framework to support the soft tissues is essential. As we have seen, none of the various skeletal patterns evolved in the invertebrates have permitted the attainment of any considerable size. Within this limitation, insects are phenomenally successful, but in

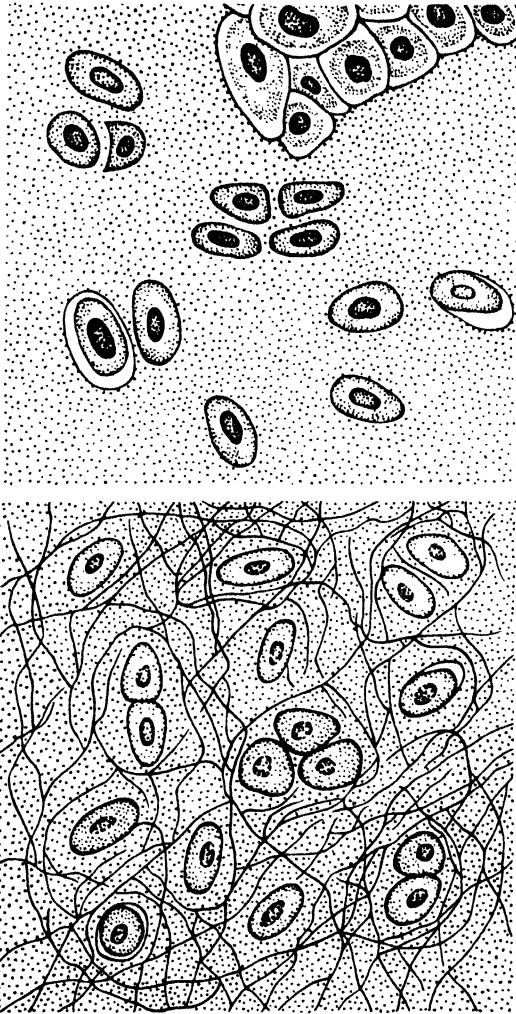


Fig. 346. Cartilage. Above: Hyaline cartilage, such as found covering the ends of bone joints. Below: Elastic cartilage, as found in the external ear.

size none approaches the average vertebrate. Size is one of the factors which determine the success of the individual, and unlike other types of framework, the vertebrate endoskeleton makes great size possible. Like other types, it gives the organism a fixed shape, provides an attachment for muscles and increases their effectiveness by acting as a series of levers, and protects delicate vital organs. But beyond these things, it grows as the rest of the body grows, and unlike a shell or an exoskeleton, it sets no absolute limit to size.

Composition of the Skeleton

The skeleton is composed of modified connective tissue, either cartilage or bone. Cartilage, perhaps more primitive, does not have the strength of bone, but it is more elastic. Lower vertebrates of the present day, and all vertebrate embryos, have cartilage only. In higher vertebrates much of the cartilage is replaced by bone as the organism matures, and cartilage remains only in places where flexibility is needed.

Cartilage consists of relatively large cells, in groups of two or more, surrounded by a continuous clear layer of moderately hard but elastic and flexible material, often reinforced with tough fibrous components. The cartilaginous mass may grow by further division and expansion of its parts (Fig. 346). Bone consists of needle-like spicules, produced by cells called *osteoblasts*. These spicules are produced in layers, with the grain of each succeeding layer deposited at a different angle from that of the last. It thus has an exceedingly tough, interwoven structure, something like laminated wood or plywood, and calcium and phosphorus deposits between the fibrous components cement it into a compact mass. It is living tissue, for the bone cells which form it remain scattered throughout its mass, and blood vessels and nerves to supply them run in canals through the bone.

A section of dense bone presents a peculiar pattern of structural units called *Haversian systems*. In any such system the bone cells are entombed within spaces called *lacunae* and surrounded by layers of spicules. Through these run fine canals, connecting the lacunae. The larger or *Haversian canals* carry the blood vessels and nerves (Fig. 347). The finer canals contain strands of protoplasm which connect the individual bone cells. Bone is rigid and incapable of expansion, but it grows by the addition of new tissue on its periphery.

General Plan of the Skeleton

In the simplest limbless aquatic vertebrates, the cyclostomes, the skeleton is no more than

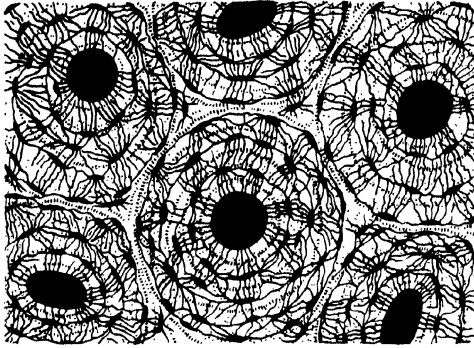


Fig. 347. Bony tissue as seen in a thin cross-section of bone. Large black centers are the Haversian canals. Small black objects in concentric rings are lacunae. Dark connecting lines are the fine canals. Concentric gray stippled and white bands are alternating layers of bone lamellae.

an articulated reinforcement built over the notochord, which still persists. In the mature forms of these lowest vertebrates, and in embryonic forms of higher ones, the vertebrae are composed of cartilage. But in the adults of higher forms, they are transformed into bone. This structure is called the *axial skeleton*. As jaws and appendages evolved, new skeletal structures developed to support them. A *visceral skeleton* supports the jaws and the breathing mechanism, and an *appendicular skeleton* supports the appendages (Fig. 348).

How the Skeleton Grows

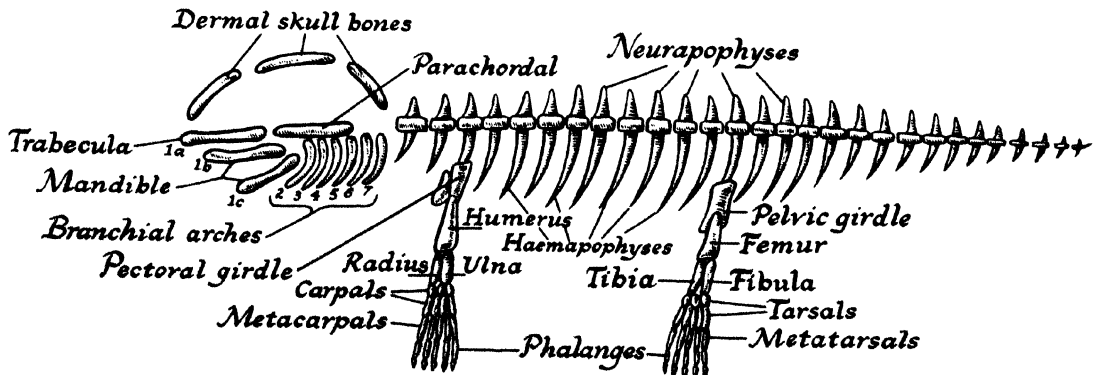
The development of the skeletal system in the embryo gives some insight into its probable evolution, though, as in so many other cases,

embryonic recapitulation is never complete and many phases may be modified, abbreviated, or even deleted.

The notochord is the first sign of the skeleton to appear in the embryo, but there soon begins to form around it a cartilaginous sheath which represents the beginning of the vertebral column. Cartilage is produced from undifferentiated mesenchyme cells which arise from a dense central streak of tissue, called the *primitive streak*, present in the early embryo. Within this tissue, the matrix surrounding the cells becomes more abundant than the cells themselves, probably due to fibers which they secrete. Further cell division within this precartilage increases its bulk by internal growth. At the same time, peripheral growth also occurs by mitosis within a sheath of connective tissue, the *perichondrium*, that surrounds the cartilage. The inner cells of the perichondrium become transformed into young cartilage cells, and these too deposit matrix and then become buried in it through their own activity, producing new cartilage.

Bone first appears somewhat later in the embryo, and two types may be distinguished: *membranous bone* and *cartilaginous* or *replacement bone*. Membranous bone is primary in the production of accessory bones in the higher vertebrates, such as the flat bones of the face and bones of the cranial vault (Fig. 349). Here the cartilaginous bone proved inadequate to the increased demands of an evolving face and brain, and entirely new bones appeared, in many instances fusing with cartilaginous bones to form new structures. Intra-membranous

Fig. 348. Stylized plan of the "typical" vertebrate skeleton. Visceral arches are numbered 1 to 7.



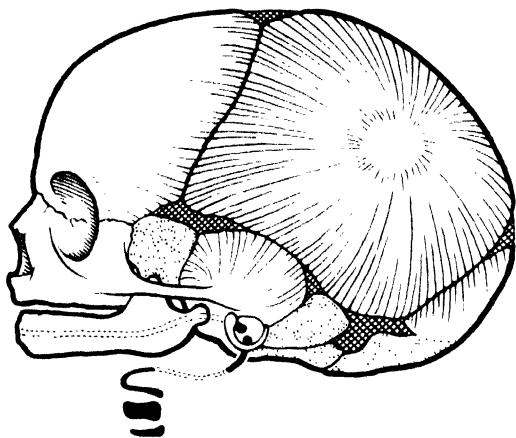


Fig. 349. Components of the human skull at birth. Membranous bones are shown white; cartilaginous bones stippled; branchial arch derivatives black; non-ossified spaces, the fontanelles, cross-hatched.

bone begins to form within relatively undifferentiated connective tissue membranes. Bone-forming cells surround themselves with spicules, to form lacunae. The whole structure then becomes encased in a *periosteum*, a membranous tissue which continues to produce new bone-forming cells; and thus growth continues. Much bone of this type is provisional and is in time reabsorbed. Certain large multinucleate cells called *osteoblasts* do this by attacking and dissolving the bone. Then new osteoblasts move in for reconstruction. In this way, even the microscopic arrangement of the bone spicules is adapted and readapted to the changing stresses and strains to which they are subject during growth.

Cartilaginous bone formation differs from this mainly in that the cartilage which it replaces is first gradually destroyed. Grooves and tubular channels are formed in it, and from bone-forming tissues penetrating these areas, cylinders or concentric layers of bone tissue develop. These are the Haversian systems (Fig. 350). In other respects the formation of replacement or cartilaginous bone is essentially the same as that of membranous bone.

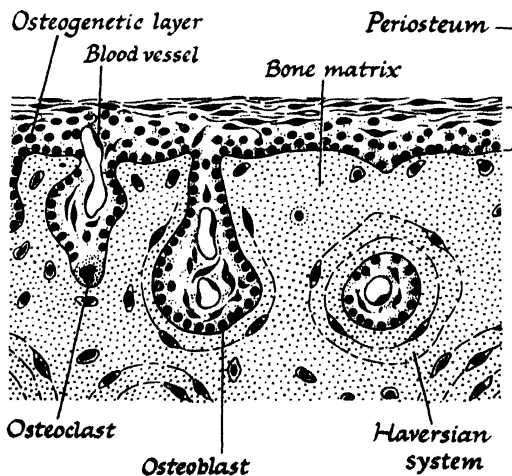
In the long bones, such as those of the arms and legs, the framework is preformed in cartilage. Near the ends of the bones, alternate cartilaginous growth and bone formation con-

tinues until the adult has attained full growth. Ossification proceeds from the center of the shafts as well as from their ends. The two zones approach each other near the heads of the bones, but here a layer of cartilage persists between them until growth of the bone is complete. By the proliferation of this cartilage, and its transformation into bone next to the shaft, the shaft becomes longer. When the bone is full-length, the cartilage becomes ossified, and growth is stopped.

Joints

Where bones meet, there is usually a union of some sort, a joint or articulation. Unions which are capable of little or no movement may occur three ways, by the formation of connective tissue between bones, as in the sutures between the bones in the top of the skull; by cartilaginous union, as between the pubic bones of the pelvis or between ribs and breastbone; or by actual bony fusion, as between the shaft and head of each long bone after the cartilage has disappeared. Moving unions, or joints, are characterized by a knob and socket surrounded by a fibrous capsule of *ligament*. The cocoon-like capsule thus formed helps to hold the bone in its socket. Between the bones there are smooth lubricating tissues, which form a fluid-filled sac or *bursa*, and frequently also a cushioning disk of cartilage.

Fig. 350. Three stages illustrating the origin of the Haversian system of bone structure.



During the formation of the skeleton in the higher vertebrates there are some startling transformations, shifts, twists, and reassignments, but the basic plan persists.

Evolution of the Skeleton

The implications of vertebrate embryology are broadly supported by fossil remains. The pre-vertebrate *Amphioxus*, though specialized in its own mode of life, still preserves the ancient notochord in almost the original form. In the degenerate but also primitive cyclostomes, primitive vertebrae of cartilage develop from separate centers above and below the notochord, and eventually fuse around it. The dorsal section of each vertebra grows upward in an inverted Y, to form a *neural arch* that envelops the nerve cord. The ventral processes produce a groove or canal, the *hemal arch*, enveloping a blood vessel; and also the ribs. In higher vertebrates, other centers of ossification take over and produce new ribs which largely replace these more ancient "fish ribs."

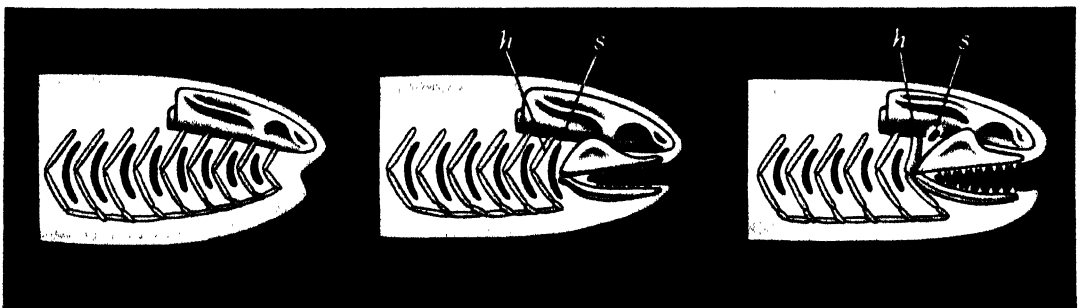
In the many fossil elasmobranchs, the neural and hemal arches and ribs are well calcified and thus well preserved, while no traces of the main body of the vertebrae remain. Presumably these bodies were present, but remained cartilaginous and so were not fossilized. From this it would appear that completely unossified forms had a poor chance of being preserved as fossils, and it is not surprising that the earliest known vertebrates had ossified skeletons. However, since ancestors of modern cartilaginous sharks appear to have had bony skeletons, we

conclude that the cartilaginous skeleton of modern sharks and rays is a degenerative rather than a primitive feature. Note, too, that the part of the bony skeleton of higher vertebrates which corresponds to the cartilaginous skeleton of lower vertebrates is replacement bone, preformed in cartilage, and the skeleton of the embryo is cartilaginous.

The specialized parts of the visceral skeleton evolved from segmentally arranged branchial arches supporting the gill slits (Fig. 351). From the primitive jawless vertebrates, represented today only by cyclostomes, jaws evolved early in fishes. The gill bars of the first branchial arches became enlarged and modified into upper and lower jaws, and then the joint of the jaw was propped against the bones of the second branchial arch and so stabilized. This also illustrates how consolidation of the visceral skeleton and the brain case of the axial skeleton began.

The development of the skull was no doubt closely related to the growth of sensory organs in the newly evolved head-end of the earliest pre-vertebrates. These organs were the *nasal sacs* or pits, the *eyes*, and the *otocysts* or ears (Fig. 352). At least, these were the sensory organs that have persisted. Skeletal plates evolved behind and under these three pairs of structures and gave them support and protection. Two at either side of the tip of the notochord supported the ear organ. A third formed beneath the eyes. At the same time, capsules formed around the sense organs themselves, and with the exception of the sclerotic coat of

Fig. 351. The evolution of jaw structures in vertebrates. Left: Jawless vertebrate. Gill arches are similar throughout. Center: One of the anterior gill bars has become jaws. The hyoid arch (*h*) is still unspecialized, as in placoderms. Right: Advanced type of jaws seen in fishes above the placoderm level. The dorsal portion of the hyoid arch has become specialized as the *hyomandibular* and braces the angle of the jaw against the brain case. Here the gill slit has been reduced to a small hole, the *spiracle* (*s*).



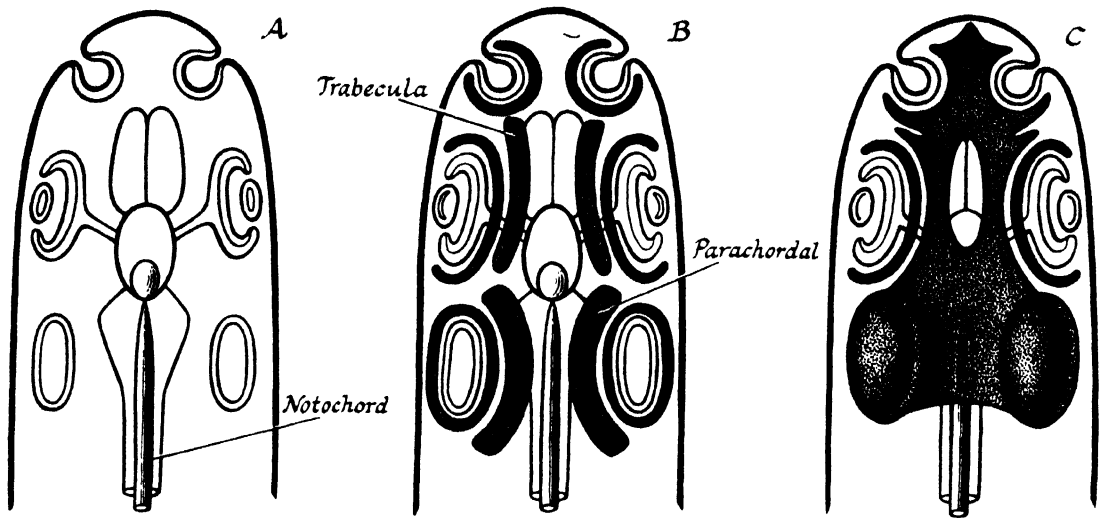


Fig. 352. Development of the primordial skull (ventral aspect). *A.* Before the appearance of cartilage. Nasal sacs, eyes, and otic capsules are present. The notochord lies below the nerve cord (above it in this view). *B.* Trabeculae (*t*) and parachordals (*p*) have formed. The sense organs have developed capsules. *C.* Capsules — except for the mobile eye — have fused with trabeculae and parachordals.

the eye, which retained its mobility, these capsules fused with the surrounding substratum, thus forming the primordial skull.

Development of the Ear

During the slow evolution from the sketchy framework possessed by the small aquatic pre-vertebrate to the skeleton of the modern masters of sea, land, and air, profound changes came about, even while the basic vertebrate pattern endured. Perhaps one of the most striking innovations was the ear. Hearing consists in a nervous response to the vibrations of air or water. It is consequently possible to hear without ears, as we can feel loud vibrations with our fingers. And in this sense, a fish can "hear," although it has only a rudimentary hearing mechanism.

Primitive aquatic vertebrates possess a "sixth sense," an ability to respond to pressure changes in the surrounding water. The seat of this sense is the *lateral-line system* of canals running along the side of the body and the head. The original labyrinthine ear may be a derivative of such a system. Embryologically, the ear evolves from an ectodermal pit which sinks into the head, leaving a duct or tube connecting with the surface. In all higher

vertebrates, this duct eventually loses its outer connection. In certain elasmobranchs, however, it persists in the adult. The *labyrinth* thus created is an irregularly shaped sac filled with liquid, lined with hairs, and containing *statoliths* or ear-stones. *Semicircular canals*, outgrowths of the sac and filled with the same liquid, continue to respond to stimulation by liquid moving within them, and so record various movements of the body. Cyclostomes have one or two semicircular canals. All higher vertebrates have three (Fig. 353).

In land vertebrates, from amphibians through reptiles to birds and mammals, the labyrinthine sacs tend progressively to bud forth a long, blind sac, which in mammals becomes the characteristically coiled *cochlea* that houses the mechanism for analyzing sounds. Thus it appears that the lateral-line pressure system of the primitive aquatic vertebrate first gave rise to the internal balancing organ, the labyrinth, and this in turn evolved into the mechanism by which a man may analyze even so complex a sound as that of a symphony.

Meanwhile other skeletal changes supported and enhanced the function of the cochlea. In fishes, the dorsal piece of the second branchial arch supports the angle of the jaw against the

brain case. Because of its position, it is not difficult to visualize how it shifted its function from support to the transmission of sound, through a closer union between visceral and axial skeleton, as in the amphibians. This bone, now transformed into the *columella*, becomes a part of the hearing mechanism. In mammal-like reptiles, the columella becomes the *stapes*, a bone shaped like a stirrup, and is adjacent to two other bones derived from the remnants of the first branchial arch, the original lower jaw. These become *incus* and *malleus* in the mammal, and with the stapes form an articulated chain of three ossicles in the middle ear, amplifying as well as transmitting the sounds from the eardrum to the window of the cochlea. (Fig. 354).

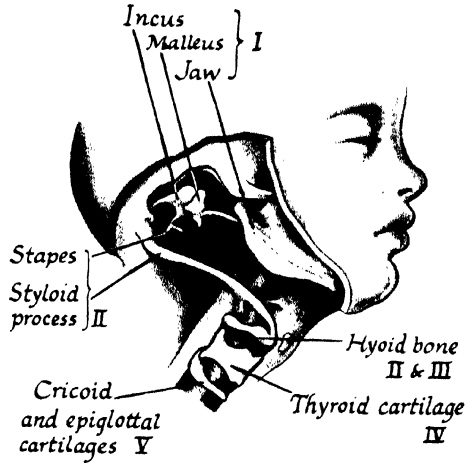


Fig. 354. Derivatives of the human branchial arches, demonstrated in lateral dissection of the head. (After Kollmann.)

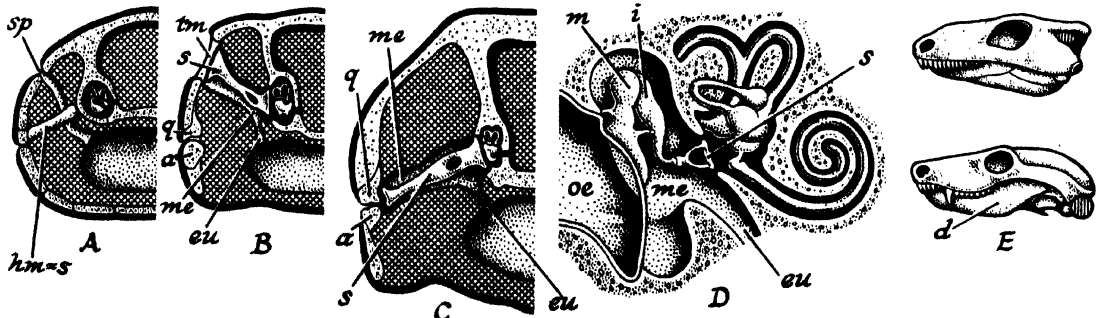
Development of Appendages

No less remarkable than the evolution of the visceral skeleton is that of the appendages, for here the vertebrate appears to have begun with nothing at all. Just how the first paired appendages in the fishes evolved is still not clear. It has been suggested that long folds on the sides of the body, used for balancing, may have appeared first; and that these then became enlarged in two regions fore and aft, while the intervening portion degenerated. In support

of this theory is the fact that the lower vertebrates have continuous dorsal fins which seem to have given rise to the interrupted ones of more advanced fishes. Also, certain primitive and extinct early fishes had as many as five pairs of supernumerary fin spines, in two parallel lateral rows.

The first paired appendages were ray-like fins in various arrangements and seem to have been used only as stabilizers. In the lobe-finned fishes, probable ancestors of the amphibians,

Fig. 353. Stages in the evolution of the ear apparatus. *A.* In the fish, the ear structure consists only of the deep-lying sacs and semi-circular canals. *B.* Amphibian. The hyomandibular bone (*hm*) of the fish is now a sound transmitter, the stapes (*s*); the first gill slit, the spiracle (*sp*), becomes the Eustachian tube (*eu*) and the middle-ear cavity (*me*), while the outer end of the spiracle is closed by the tympanic membrane (*tm*). *C.* A mammal-like reptile. The stapes passes close to two skull bones (*q*, quadrate; *a*, articular) which form the jaw point. *D.* Man (the ear region only, on a larger scale). The two jaw-joint bones have been pressed into service as accessory ossicles, the malleus (*m*) and the incus (*i*). *E.* A primitive land animal and a mammal-like reptile show the relation of the eardrum to the jaw joint. At first in a notch high on the side of the skull, it shifts to the jaw region. In mammals the jaw is formed of one bone only (*d*, dentary), and the bones of the jaw-joint region are free to act as accessory hearing organs; *oe*, tube of outer ear.



THE DRIVING MECHANISM: THE MUSCULAR SYSTEM

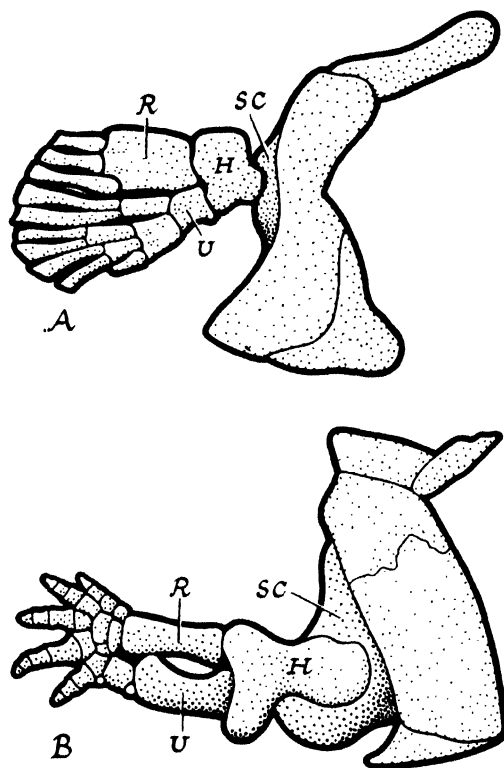


Fig. 355. A. The pectoral girdle and fin of a lobe-finned fish, the Devonian crossopterygian *Sauripterus* (after Gregory). B. Diagrammatic representation of a quadruped limb placed in a comparable position. h, humerus; r, radius; u, ulna, sc, scapula.

the skeletal pattern of the appendages strongly resembles that of the future land vertebrates, so that there can be little doubt that such fins became legs (Fig. 355).

True to their origin, the first amphibian legs were on the sides of the body, and because they spraddled, were woefully insufficient as body supports (page 128). Strong and bulky girdle attachments were needed to fix them adequately to the axial skeleton. Finally, in mammals the hind legs were rotated so that the knees pointed forward, and the front legs were rotated in the opposite direction, so that the elbows point backwards. In both cases the legs were thus pushed under the body to serve as pillars, rather than bridge-spans, and the girdle supports were reduced.

Because of their aggressive feeding habits, most animals move about actively, and 40 to 50 per cent of the body weight of many of them may consist of "flesh" or muscle. Muscle performs many functions. It often determines shape, it supplies movement for locomotion, and it provides the major part of the movement necessary for respiration, nutrition, excretion, and reproduction. The ability of tissue to contract is not new, nor is it limited to muscle. But in undifferentiated protoplasm contraction appears to operate in many directions, whereas in muscle tissue it is polarized along a specific axis, so that its efficiency is greatly increased. The cell itself is oriented on this axis, and frequently all the cells within a group or bundle are similarly oriented. These bundles, of varying sizes, are powerful contracting units, capable of moving the bones to which they are attached with great force. Under the control of hormones or the central nervous system, the movements of the whole body and of its parts are synchronized. Evolution in vertebrate muscle lies in the elaboration of muscle groups rather than in any fundamental changes in muscle tissue. The greatest evolutionary advance in the mechanism of motion lies not in the muscles, however, but in the elaboration and refinement of the nervous system which controls them. We may therefore consider our study of muscles as applying to all vertebrates, including man.

Types of Muscles

Muscle cells contain specialized protoplasmic strands which perform the actual contraction. These lie in a more fluid medium, and surrounding the whole is a tubular sheath. The relative proportion of the fluid to the strands varies according to the function of the muscle.

There are three types of muscle tissue: (1) *smooth muscle*, also called visceral or involuntary; (2) *striated muscle*, also called skeletal or voluntary; and (3) *cardiac muscle*, also referred to as indistinctly striated.

Smooth muscle, the most primitive type, is composed of simple spindle-shaped cells (Fig. 356). In vertebrates it is the common muscle of the skin and viscera (intestines, stomach, blood vessels, etc.) and is not under voluntary control. Significantly, the muscles of invertebrates, with the exception of the arthropods, are almost exclusively of this type though some jellyfishes have striated muscles in parts requiring rapid motion. Smooth muscles are relatively slow to react, and their contraction period is slow and long. In the stomach muscles of the frog, the lapse of time between stimulus and response may vary between $1\frac{1}{2}$ and 10 seconds, and a contraction may take as long as 120 seconds.

Striated muscle is syncytial, and the nuclei are close beneath the sheath. The fibrils, lying within the fluid in parallel bundles, show a peculiar zebra-like striation. Such fibers differ in the proportion of sheath to fibrils. Some are densely packed and have little fluid. These are termed white muscle fibers, and are found in muscles which react rapidly, like most body muscles. Others, with relatively few fibrils and rich in fluid, are called red muscle fibers. These react more slowly but have greater endurance. They are found in the extrinsic eye muscles, in the diaphragm, and in such muscles as those which control the ceaselessly beating dorsal fins of the sea horse. Among birds, strong fliers, in contrast to poor ones, have muscles well supplied with fluid. Thus the flight muscles

in the breasts of strong fliers such as ducks and pigeons are dark (red), while those of chickens are white. Striated muscle may complete its contraction in .04 second.

Cardiac muscle shows certain features of both these types. It is striated, but with special features. The fibers run continuously through protoplasmic bridges from cell to cell, so that the entire heart is a continuous syncytium, a network with narrow meshes stretched in one direction. Thus it is enabled to function as a unit. Cardiac muscle is always well supplied with fluid (sarcoplasm), in keeping with its great powers of endurance.

General Plan of Muscle Tissue

Since muscles work only by contracting, a contracting muscle must be restored to its original state before it can act again. This is usually accomplished by a second muscle operating as an antagonist to the first. Thus the biceps flexes the arm at the elbow; the triceps extends it again, and in the process, the biceps is brought back to its original form and position. Muscles of the intestine are in two (or more) distinct layers, longitudinal and circular, much as in the earthworm. The former shorten the intestine and increase its diameter, while the latter decrease the diameter, by this action accomplishing most of the work of the intestine. Some muscles have as antagonist a counter pressure. Thus the diaphragm flattens out when it contracts, and when it relaxes it is

Fig. 356. A. Smooth muscle tissue. B. Striated muscle tissue. The full length of the cells cannot be seen since striated muscle cells are longer than the microscopic field. C. Cardiac muscle tissue. Note the branching nature of the cells; also the cross striations.



pushed back into its original dome-shaped form by the greater pressure from the abdominal organs below.

Antagonistic muscles are usually not equally matched in strength. The muscles of the forearm which close the hand are considerably stronger than those which open it. This is why the general muscle contraction induced when a hand grasps an electrically charged wire causes it to clutch the wire despite the wish to let go. Likewise, the circular muscles of the intestine are far more powerful than the longitudinal ones, and the wing depressors of a bird exceed the strength of the lifters by as much as fifty times. An unusual complex of antagonistic muscles is found in the tongue. Fibers criss-crossed like those in felt account for the great flexibility of which this organ is capable.

Most muscles are attached at opposite ends to separate bones which may be moved with respect to each other like a hinge. Tough connective tissue forms a sheath that covers and penetrates each bundle of muscle fibers. Towards the tapering end of a muscle, the connective tissue increases in quantity and merges into a dense white cord, the *tendon*. Near the bone, this merges with the periosteum, the connective tissue sheath of the bone itself.

Muscle Action and Body Temperature

Muscles are never completely at rest, but are always in a state of partial contraction called *tone*. This condition not only provides the necessary postural stability during waking hours, but continues even in sleep. Indeed, the release of heat during muscle contraction is the chief source of the body temperature of warm-blooded animals. That this is so can be demonstrated by canceling all motor stimuli to muscles, as for example by the use of such nerve poisons as the South American arrow poison, *curare*. An animal injected with this drug becomes completely limp, and all muscle activity ceases. Consequently, its temperature drops to that of its environment and rises again only if the outside temperature rises. It has thus lost its ability to maintain a high and stable body temperature, and in this respect its reac-

tions become like those of cold-blooded animals. Similarly, continued or rapidly repeated stimulation produces a state of constant and increasing reaction called *tetanus* or *tetanic contraction*. Like muscle tone, this is a result of the repeated explosive reactions of the individual muscle fibers in the muscle, acting in relays. Since the mechanism of muscle contraction is only about 40 per cent efficient, 60 per cent of the unleashed energy is released as heat. Before this is judged to be a low degree of efficiency, it ought to be noted that it is several times better than that of most internal combustion engines.

Muscle Contraction

Most of the work of the body and all the work of muscles is accomplished by the shortening of muscular fibers. This seemingly simple process has been subject of research for many years, but is not yet fully understood.

Muscular contraction results from a complex chain of chemical reactions, some of which take place with explosive speed, within the individual muscle fibers. Each fiber may be compared to a loaded cartridge, with a store of available energy lying ready to be released in response to the proper stimulus. Too weak a stimulus will produce no response at all, but when the stimulus becomes strong enough, the full store of energy is released all at once, so that a stronger stimulus would have released no more. This principle of response is referred to as the *all-or-none law*. Repeated contraction of the fiber is impossible until a new supply of energy has been provided, but irritability is quickly recovered. Indeed, the entire cycle of contraction and relaxation occupies but a fraction of a second.

The shortening of a muscle fiber appears to result from a contraction or folding of the chain-like protein molecule *myosin*, which constitutes most of the muscle fiber. In some manner, this contraction is related to the catabolic transformation of a substance called *adenosine triphosphate*, which results in a release of phosphoric acid. Energy thus released appears to be the direct source of power in the

contraction process. It is interesting to note that this is an *anaerobic* process, and that consequently a muscle can contract even if deprived of oxygen. But its power to do so quickly declines as the available supply of the organic phosphate disappears. Another anaerobic reaction closely associated with muscle contraction is the breakdown of glycogen into lactic acid through the intermediation of the organic phosphates. This process yields energy which may be utilized to resynthesize the original organic phosphate from the fragments resulting from its earlier catabolism. In the presence of oxygen, 20 per cent of the lactic acid thus formed is oxidized into CO_2 and H_2O , and the energy realized from this is utilized to transform the remaining 80 per cent of the lactic acid back into glycogen. The muscle fiber is thus restored to its original condition, ready for instant contraction again.

The ability of an organism to display a burst of energy considerably beyond its capacity to release it by oxidation within so short a span of time, is based upon the ability of a muscle to contract anaerobically. The organism simply draws upon a store of energy accumulated by previous oxidative processes. This accounts for the fact that after violent exertion, an animal will continue to breathe heavily for a considerable period, for it is simply repaying its oxygen debt and restoring the balance of glycogen which it had to start with. The inability of muscle to respond beyond certain demands which produce fatigue lies in the disappearance of glycogen and organic phosphate and in the accumulation of lactic acid, which characteristically sets up the state of fatigue. The ability of an organism to perform vigorously and steadily thus depends on a sufficient blood-sugar supply, good circulation, good respiration, activity commensurate with the amount and quality of its muscle tissue, and, wherever exertion is violent, periodic rest to allow restoration of energy-yielding compounds.

Failure to use a muscle results in its degeneration, the destruction of nerve centers or motor nerves, and even the loss of muscle tone. When this occurs the muscle tissue wastes

away, as in infantile paralysis. Treatment designed to maintain some degree of activity can sometimes prevent this kind of degeneration.

How Muscle Grows

The three types of muscle differ in origin as much as in form. Smooth muscles are formed as parts of the organs in which they develop, arising from loose mesodermal tissue, the mesenchyme. The cells of the future muscle enlarge and elongate. Additional cells may be produced by mitosis of the first-formed fibers as well as by differentiation of additional mesenchyme cells on the outside.

Cardiac muscle develops from the mesoderm surrounding the blood vessels from which the heart originates. Skeletal muscle is derived from myotomes, each a part of a segment of the early embryo, corresponding to a somite of *Amphioxus*. Some skeletal muscles of the head and neck are derived from the mesenchyme of the gill arches. In keeping with the segmental plan of vertebrates, the myotomes are arrayed, a pair to each segment, on either side of the notochord. This primitive segmental arrangement is soon lost in most higher vertebrates, but in lower ones it may persist to a considerable degree throughout life (Fig. 344). In all cases, the segmental arrangement of the spinal nerves which serve the muscles persists, indicating the original segmentation.

In higher vertebrates, such as man, in contrast with the lower vertebrates, there is considerable fusion of myotomes and "migration" of muscles. Thus the large sling-like *latissimus dorsi*, which first appears in the neck of the embryo, later becomes attached to the inner surface of the arm near the shoulder joint, passes beneath the armpit and down the back, and attaches to the lower vertebrae. The original metamerism is often all but obscured by later changes brought about through the increasing importance of the appendages.

THE NERVOUS SYSTEM

Coordination — beyond the most elementary form of the transmission in all directions of a

state of excitation — does not seem to be an inherent property of protoplasm, for even in protozoans special structures perform this function. Thus in *Paramecium*, differentiated protoplasmic strands coordinate the action of the cilia (Fig. 221). How much more important is a coordinating system in an organism consisting of millions of cells!

In the vertebrate two distinct yet closely interrelated systems achieve integration, the nervous system and the endocrine system. The two are closely interrelated both anatomically and functionally. The coordinating agent of the nervous system is the nerve impulse — an electrochemical change propagated along the enormously elongated cell units of the system, the *neurons*, in the form of wave-like surges. The coordinating agents of the endocrine system are purely chemical, and consist of specific compounds made in certain glands and called *hormones*, which are distributed throughout the body in the blood stream.

Through the nervous system specific impulses can be conveyed to any of thousands of struc-

tures with exquisite precision, and in a fraction of the time it would take hormones to reach these structures. Both systems are capable of diffuse as well as specific action, but in general the nervous system is the more specific, localized, and precise.

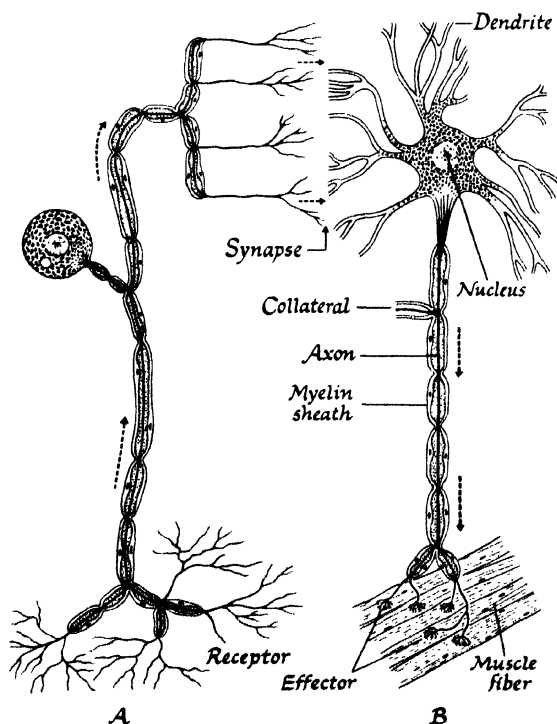
As was said earlier, the nervous system in higher animals may be compared to a modern centralized telephone system, whereas that of more primitive animals is comparable to the old-fashioned circuit in which a ring brought a response at every phone on the circuit.

The sequence of events in the centralized nervous system is: (1) reception of a stimulus from inside or outside the body, (2) transmission of the excitation to the central nervous system by nerve fibers, (3) selective relaying of the impulse to the proper motor centers, and (4) transmission of the impulse outward to the effectors, either muscles or glands. The receptors include all the structures which respond to stimuli coming from outside the nervous system itself — the eye, ear, nose, and taste buds — and the organs of general sense, located in the skin, muscles, or internal organs. In the latter, there are simple nerve endings or specialized structures supplied with nerve endings, for the reception of stimuli such as pressure, pain, chemical change, heat, and cold.

Nerves, which carry nerve impulses, are relatively thick, white cables consisting of hundreds of individual nerve fibers, each a minute strand, all held together by sheaths of connective tissue. The telephone analogy may be applied here, too, for a nerve corresponds in structure and function to a cable consisting of hundreds of insulated individual wires in a protective tube.

It is a somewhat astonishing fact that most vertebrates are capable of only two kinds of response: movement and secretion, and that the effectors are limited to muscles or glands. A few vertebrates are capable of other responses, such as the production of high-voltage electricity. These are the electric eels and the torpedo, an electric ray. Yet this response is not basically new, for every cell responds to stimulation by producing an electric current, though usually one so feeble that it creates no

Fig. 357. Diagrams of two types of neurons.
A. Sensory neuron. B. Motor neuron.



noticeable effect outside its own cell body. A few fishes also produce light.

The Neuron

The minute strands which compose a nerve are elongated processes of cells called *neurons*. A neuron consists of three main parts: (1) the cell body, containing the nucleus, (2) *dendrites*, root-like processes of the cytoplasm which increase the receiving surface of the cell body, and (3) an *axon*, an elongated process of the cell which carries the nerve impulse from the cell body to the next station in the relay (Fig. 357).

Dendrites are thick, short, often many-branched processes, and axons — of which each neuron usually has only one — are much longer, are smooth, slender, and little branched, except at the very end. An electrically insulating fatty coat, the *myelin sheath*, surrounds many axons.

Types of Neurons

There are two distinct types of neurons in the peripheral system, *sensory* and *motor*. Sensory neurons transmit impulses from peripheral sense organs to the spinal cord. The cell bodies of these form clumps, the *sensory* or *dorsal ganglia*, just outside the spinal cord (Fig. 359). Motor neurons carry impulses from the central nervous system to the muscles and glands. The cell body lies within the spinal cord, and only the axon projects beyond it. The terminus of the axon on a skeletal muscle consists of a branched network of fibers known as a motor end plate (Figs. 357 and 359).

Within the central nervous system, there are many kinds of neurons (Fig. 358). The highly specialized types are especially characteristic of the brain. *Connecting* or *associative* neurons, found in the spinal cord, appear to be relatively simpler and less specialized. These connect sensory and motor neurons or associate them with higher and lower centers of the nerve cord and with the brain.

Synapses: Neuron Connections

Each neuron is a subordinate member of a system, and the nerve impulse it carries must

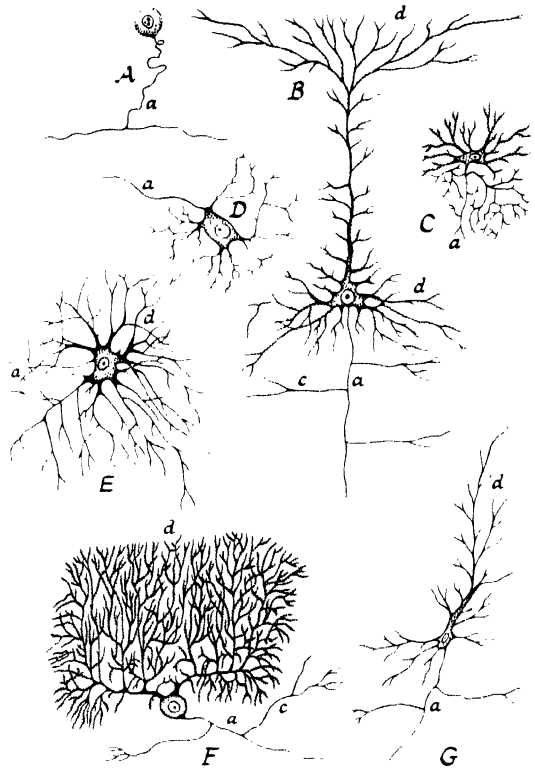


Fig. 358. Varieties of neurons of the human nervous system. *A.* From the spinal ganglion. *B.* Pyramidal cell from cerebral cortex. *C.* Golgi cell from spinal cord. *D.* Small cerebellar neuron. *E.* Spinal neuron from anterior horn. *F.* Purkinje cell from cerebellar cortex. *G.* Fusiform cell from cerebral cortex. *a*, axon; *d*, dendrite; *c*, collateral branches. (Morris, *Human Anatomy*, The Blakiston Co., Publishers.)

be transmitted to others before there can be a response. Neurons are generally distinct units, with no protoplasmic continuity between them. Where the axon of one approaches the dendrites of another, it breaks up into many fine fibers which end in minute swellings (the *boutons*), which touch the dendrites or the cell body of the neuron next in line. The contact zone is the all-important *synapse*, which plays the role of switchboard operator, for it somehow determines whether a given impulse will pass on or not.

A nerve impulse is set up by the excitation of a receptor, passes along a sensory neuron into the spinal cord, and is transmitted across the synapse to an association neuron. A new nerve impulse then passes through the association

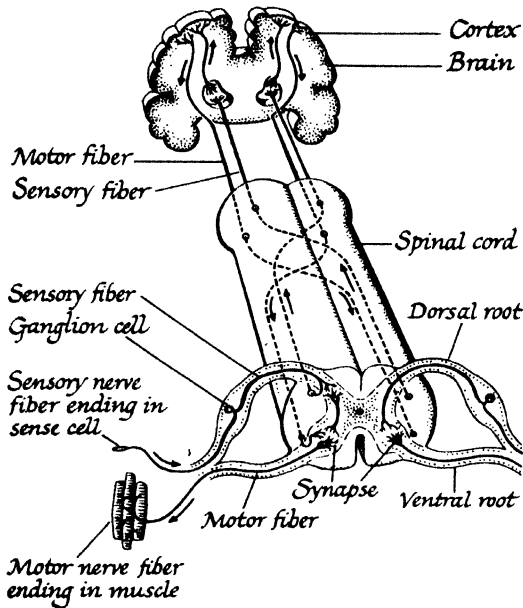


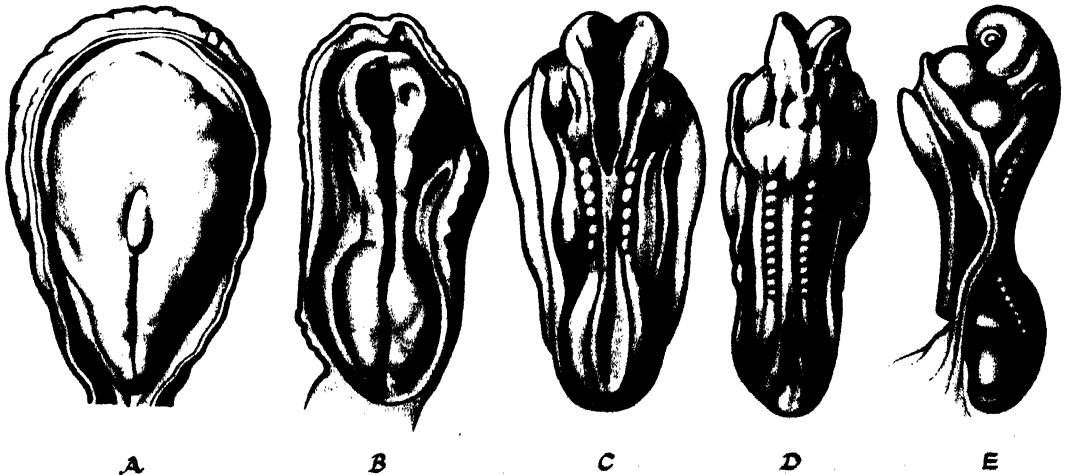
Fig. 359. Diagram of the paths of sensory and motor nerve fibers.

neuron across the synapse to a motor neuron, and another new impulse goes through this to the muscle or gland, which makes its typical response. Such a path, involving only the spinal cord, and not necessarily the brain, is called a *simple reflex arc* (Fig. 359). But the reflex is not usually so simple as described, for axon branches usually connect with dendrites of many neurons. Thus the original impulse

may arouse impulses in an intricate system involving many association and motor neurons and a corresponding number of effectors.

An impulse transmitted to the central nervous system through a particular sensory neuron does not always bring about the same reaction, and here the synapse comes into play. Previous events in the nervous system, determined by previous experiences, may radically alter the ease with which an impulse crosses a synapse. Thus a stimulus causing one reaction under one set of conditions may cause quite a different reaction if conditions are changed. It is in the synapse that we must seek an explanation for the variety and intricacy of behavior. And it is probably in the complex interplay of synaptic changes in the brain that we must seek an understanding of learning and reasoning. Older notions of the nervous system as a series of paths some of which become "well beaten" because of the continual passage of impulses, must be modified in the light of current knowledge. Among the evidence that forces such a changed viewpoint are the observations that (1) no one nerve tract is responsible for the passage of a specific reflex every time it occurs; (2) no such permanent and radical change in a nerve tract as would be implied by the path analogy has ever been found; and (3) a nerve tract may operate in the service of different reflexes at different times.

Fig. 360. Development of human neural tube and groove (Streeter). All but *E* are in dorsal view. *A*. Pre-somite embryo, with neural plate and primitive streak. *B*. Somites forming; deep neural groove. *C*. Seven somite stage; neural tube beginning to close. *D*. Ten somite stage; brain region beginning to close. *E*. At nineteen somites; closure complete except for neuropores.



Growth of the Nervous System

The central nervous system of the vertebrate, like that of *Amphioxus*, is derived from a tube made by an infolding of ectodermal tissue. As the thickened neural plate gradually sinks below the level of the ectoderm to form a neural groove, a strip of cells begins to differentiate at the juncture of this groove and the general ectoderm. These are the cells of the *neural crest*, destined to form the cranial and spinal ganglia (of the sensory nerves). The neural tube now closes, beginning at the middle and progressing toward both ends (Fig. 360). The anterior end grows more rapidly, and somewhat unevenly, to form three bulbous enlargements, the primary vesicles of the brain (Fig. 361) the *forebrain*, the *midbrain*, and the *hindbrain*. The first and last of these divide again, thus establishing the five primary divisions of the vertebrate brain (see table, page 404). The re-

mainder of the tube becomes the spinal nerve cord.

Development of Neurons and Supporting Tissue

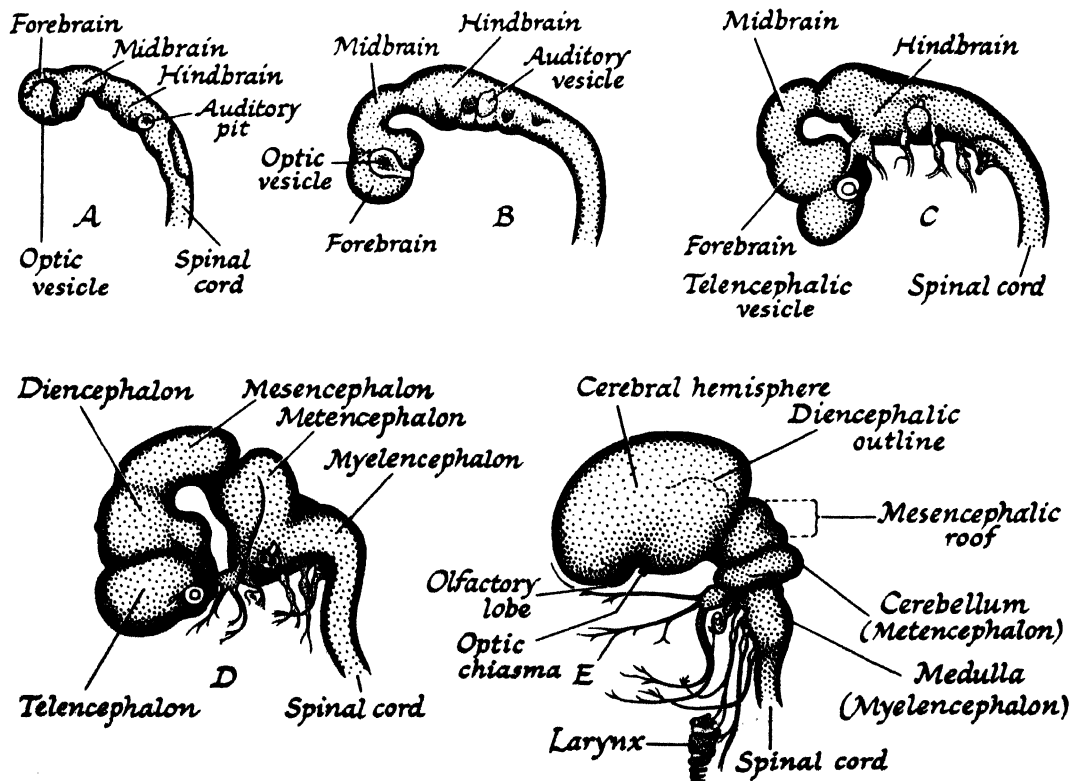
When the neural tube closes, it consists of a thick mass of cells, partially syncytial. The innermost ones give rise to lining and supporting cells called *neuroglial tissue*, and to *neuroblasts* which differentiate into neurons. Further supporting tissue is derived from other parts of the tube.

Neuroblasts generally each produce an axon and dendrites at opposite poles, thus becoming *bipolar cells*, but in those of the neural crest, two processes move around to one side of the cell and merge for a short distance, thus producing the typical unipolar sensory nerve cell.

The Cord and the Brain

The anterior portion of the neural tube forms the brain, but the greater portion becomes the

Fig. 361. Development of the human brain, five stages (Patten). A. 3 mm. B. At 4 mm. C. At 8 mm. D. At seven weeks. E. At three months. In B and C, the parts labeled "forebrain" are telencephalon and diencephalon respectively. In C the "hindbrain" is developing into metencephalon and myelencephalon.



spinal nerve cord. Some cells of the tube differentiate into association and motor neurons, so that the synaptic connections between these arise in this region. The sensory neurons, it will be recalled, originate and remain outside the cord in their own sensory ganglia. The gray region of the cord becomes surrounded by a white mass, made up of the axons of association neurons transmitting impulses the length of the cord, and the fibers of sensory or motor neurons entering or leaving the cord. Thus the *gray matter* represents the area of cell bodies and synapses, and the *white matter* consists of nerve fibers and their sheaths. The gray portion of the cord consists of four lobes, radiating from the central position of the original cavity of the neural tube, which becomes

greatly reduced. The proportion of white matter to gray varies from region to region, since the quantity of gray matter is largely determined by the amount of effector tissue to be served at that level, whereas the white matter increases toward the head end, since all fibers connecting the body with the head have to pass through the neck.

Evolution of the Vertebrate Nervous System

So far as is known, there have been few marked changes in the basic arrangement of neurons and their connections since the earliest chordate stages of evolution. However, the spinal cord reflects the mode of life and the activity of its possessor. Although there is no evidence of metamerism within the cord, the

DIVISIONS OF THE VERTEBRATE BRAIN

PRIMARY VESICLES	SUBDIVISIONS	DERIVATIVES	PRIMARY FUNCTIONS
Forebrain (Prosencephalon)	Telencephalon	Corpora striata Cerebral cortex† Rhencephalon	Complex reflexes Voluntary motor actions Sense perceptions Learning. Memory. Association Olfactory lobes. Chemical sense. Smell
	Diencephalon	Epiphyses Thalamus Hypothalamus Posterior lobe of hypophysis Mamillary bodies Optic chiasma	Pineal and parietal bodies. Possibly endocrine Relay station to cortex Emotional center? Sleep center? Endocrine
Midbrain (Mesencephalon)	Mesencephalon	Optic lobes* Corpora quadrigemina†:‡ 2 superior colliculi 2 inferior colliculi	Vision Muscular reflexes: eye and pupil Audition (hearing)
Hindbrain (Rhombencephalon)	Metencephalon	Cerebellum Pons†	Coordination of voluntary muscular activity Bridge connecting two sides of cerebellum, and cerebellum with cerebrum
	Myelencephalon	Medulla	Reflex center for automatic activities (respiratory)

* In lower vertebrates only.

† In higher vertebrates only.

‡ In mammals, optic lobes differentiate into corpora quadrigemina.

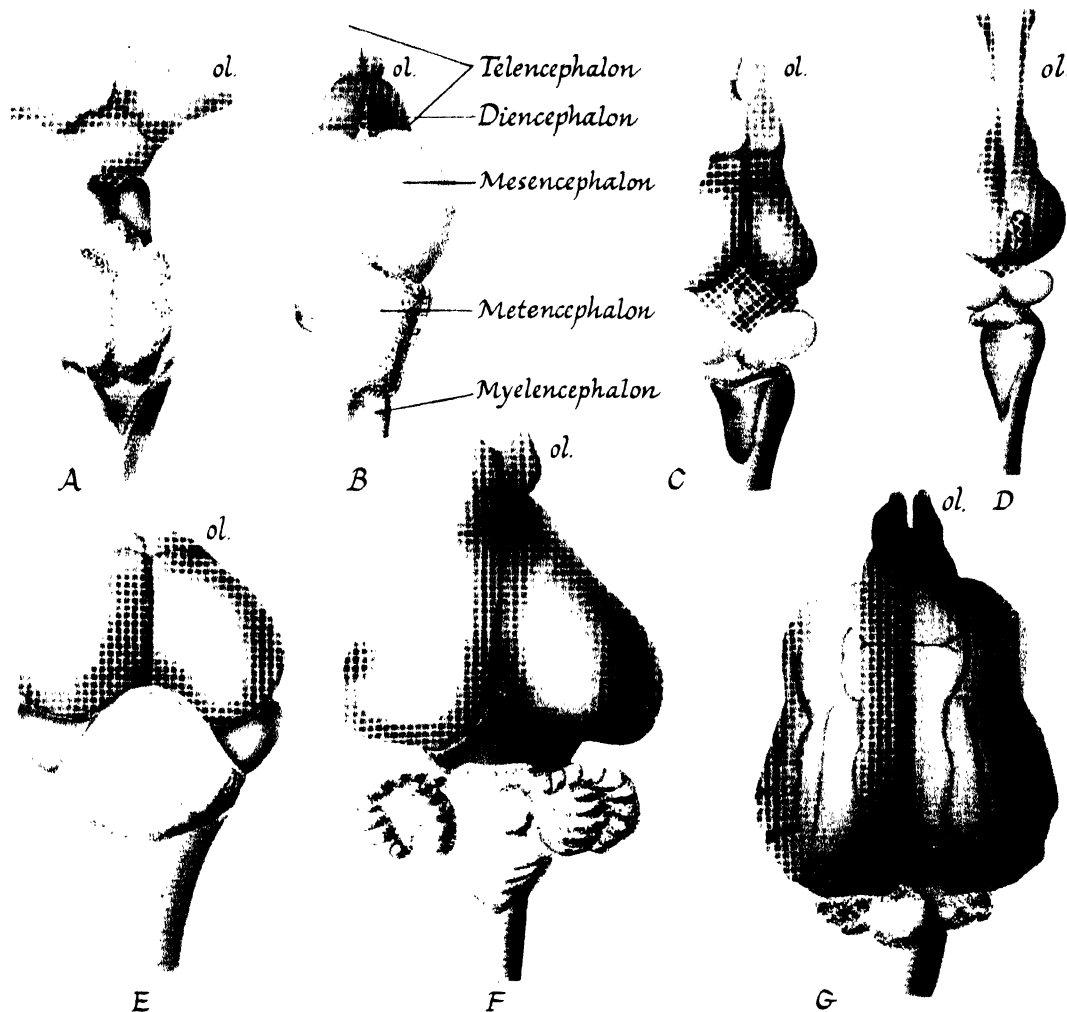


Fig. 362. Vertebrate brains, dorsal view. A. Shark (*Scyllium*). B. Bony fish (salmon). C. Amphibian (frog). D. Reptile. E. Bird (pigeon). F and G. mammals (rabbit and dog). ol, olfactory lobes. Scheme of identification is illustrated in B.

spinal nerves which emerge from it are arranged segmentally. Cyclostomes and fishes lack that sharp distinction between white and gray matter to be found in the higher vertebrates. Also, in fishes, the sensory neurons remain bipolar like those in the early developmental stages of higher vertebrates, and thus are primitive.

The development of appendages in land vertebrates is mirrored in the structure of the cord. In fishes it shows little local differentiation, but in limbed vertebrates there are distinct swellings in the limb regions, due to the

accumulation of motor neurons there. These are especially marked in turtles, where the muscles of the trunk have atrophied after the ossification and fusion of the ribs with the shell had rendered them useless. In the dinosaur *Stegosaurus*, the enlargement of the spinal cord in the pelvic region was twenty times the size of the brain.

Nervous reactions at the spinal level, *i.e.*, reflexes which involve only three neurons, are efficient and have changed little. But as the brain-centered system evolved, the brain became larger because many simple reflexes were

integrated to form, in effect, super-reflexes. A second factor that augmented brain size was the increase in importance of the special sense organs at the head end of the animal and the parallel increase in the brain centers serving them. The ratio of brain to nerve cord in *Stegosaurus* suggests that it had not progressed very far in this direction.

The higher we go on the evolutionary tree, the larger is the brain in relation to the cord. Assigning to the cord a unit mass of 1, we find the following relative brain masses: salamander, 0.9; frog, 1.0; cow, 1.5; rabbit, 2.0; cat, 4.0; monkey, 8.0; man, 26.0. These figures are even more significant if we compare actual weights in animals of similar bulk and activity, such as a cat and a small monkey having the same body weight:

	<i>Cord Weight</i>	<i>Brain Weight</i>
cat	7.5 gr.	29 gr.
monkey	7.5 gr.	62 gr.

Moreover, in different vertebrates different regions of the brain show varying degrees of development in relation to the rest, though there is no simple direct trend of development in this respect (Fig. 362). Instead, the diverse specialization of eyes, nose, or general coordination is reflected in the corresponding brain areas. Thus even the human brain is clearly inferior to that of most other mammals in the size of its olfactory lobes and associated areas, which determine the ability to smell. The shark has enormously developed olfactory lobes. The salmon, a bony fish, is inferior in this sense, but has strongly developed optic lobes. In the amphibians, smell once more dominates sight, as it does in some reptiles. In birds, the olfactory lobes are feebly developed. In birds and mammals a great swelling of the forebrain, the cerebrum, begins to dominate the brain. In primates especially, all parts of the brain are subordinated to the cerebrum, the learning center which enables them to adapt to novel situations and hence "to live by their wits."

Shift in Control

In the increasing importance of the brain two trends are noticeable: *cephalization*, the dominance of the head region and the gradual shift of control to the brain; and *corticalization*, the increasing degree of control by the cerebral cortex, or outer layer of the cerebrum.

Location of the brain and sense organs in the head is probably no mere coincidence. Beginning with the crowding of neurons around the mouth region of hydra, the increased sensitivity of this region no doubt increased its selective value. It is logical for this end of the animal to lead the way in subsequent explorations of its environment. Thus the mouth end becomes the head end, and the head end becomes the center for organs of special sense.

The gradual shift of control to the brain is well illustrated by the behavior of "spinal animals," in which the brain has been destroyed or severed from the spinal cord. The "spinal" frog still hops, scratches, and swims in response to adequate stimuli, quite like a normal frog. A "spinal" reptile shows similar unconcern. Their behavior patterns are largely organized within the spinal cord. But "spinal" birds and mammals are pathetically helpless. They can still perform simple reflexes like the extensor reflex, in which extensor muscles respond to pressure on the foot pad; but the organization of these reflexes into a coordinated action such as walking is entirely lost. At this evolutionary level, walking has come under the control of the brain and is flexible and adaptable.

As the cerebrum develops, it takes over functions previously centered in the lower nervous regions. Removal of that hindmost part of the cerebral cortex which is concerned with vision, the *visual cortex*, results in only a slight impairment of vision in rats. They can still distinguish both patterns and degrees of illumination. Monkeys similarly treated can still discriminate between degrees of brightness, but not between patterns. But man, in whom corticalization has reached its peak, becomes totally blind. The gradual transfer of visual centers from the midbrain to the cortex may

be clearly grasped by comparing differences between even more widely separated vertebrates, such as a fish, reptile, and mammal (Fig. 363).

Final evidence of increasing corticalization in mammals is given by Sperry's experimental muscle translocations. In groups of rats, flexors and extensors were transposed in both hind and fore legs so that an attempt to flex a muscle would produce extension, and vice versa. These rats in time learned to use their fore legs as stiffened crutches by contracting both flexors and extensors, but they never learned to shift responses, and they never learned to use their hind legs at all. The difference is to be explained by the fact that the fore legs are under cortical control more than the hind legs. In man cortical control has reached the point where he can, by dint of intense concentration, learn to control almost every individual muscle. The resultant increase in versatility and adaptability is obvious.

The Autonomic Nervous System

The portion of the vertebrate nervous system concerned with visceral control is rather misleadingly called the *autonomic nervous system*. For it is not anatomically separate, nor is it, strictly speaking, autonomous. It consists of two rows of connected ganglia, one on each side of the nerve cord, somewhat like the rows of sensory ganglia. The autonomic ganglia are anatomically a part of the cerebro-spinal system, but function to a large degree independently of the higher nervous centers. This "system" is divided into two functionally different parts: (1) the *sympathetic*, which stimulates the activities of many structures over which we have no voluntary control, such as the heart and the muscles of the blood vessels, but inhibits activity in the stomach, intestines, and so on; and (2) the *parasympathetic*, which reverses the effects of the sympathetic. Between the two, normal activity and rhythm of the viscera are maintained. Parasympathetic nerve fibers arise chiefly in the ganglia of the cranial and sacral regions, sympathetic fibers mainly in the thoracic and lumbar regions.

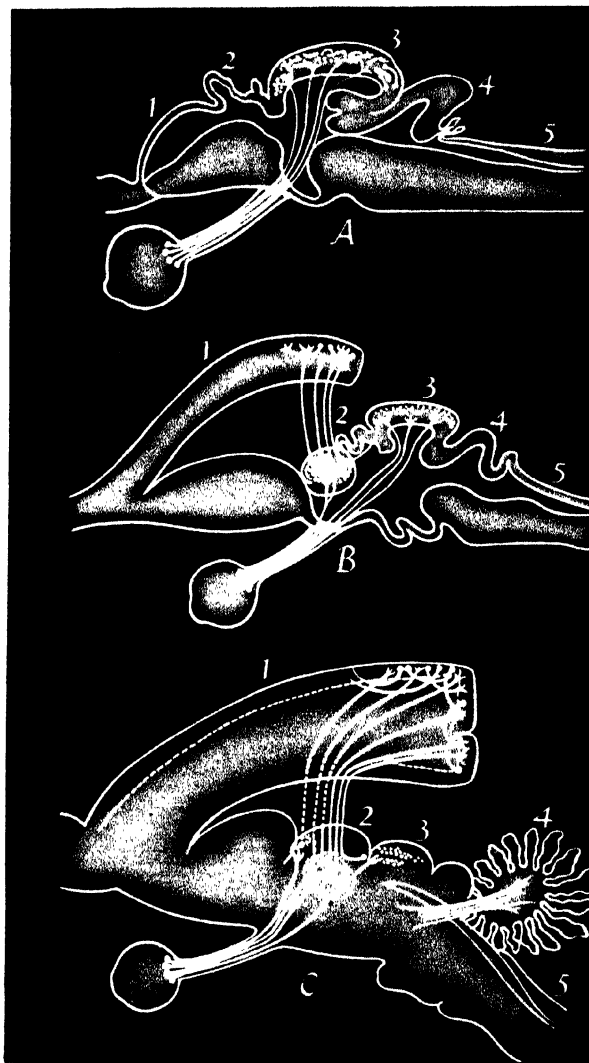


Fig. 363. Shift in visual centers from the metencephalon to the cerebral cortex. Paths of optic nerves and associating neurons are shown. A. Fish. B. Reptile. C. Mammal. 1. Telencephalon. In B and C it becomes cerebral cortex. 2. Diencephalon. 3. Mesencephalon. 4. Metencephalon. 5. Myelencephalon.

Anatomically, the autonomic system is intimately connected with the cerebro-spinal system. Afferent sensory fibers pass from the viscera through the sympathetic ganglion and enter the cord through the dorsal root (Fig. 364). The cell body of such neurons lies in a dorsal root sensory ganglion, and not in a sympathetic ganglion. Also in the spinal cord are motor neurons called pre-ganglionic neurons, because their axons pass out through the ven-

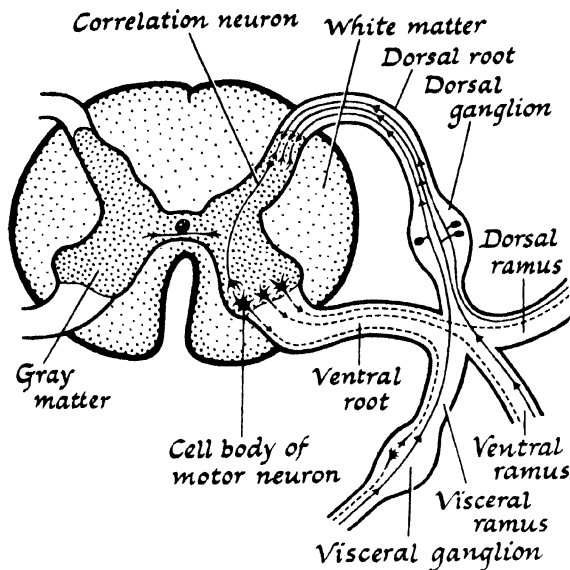


Fig. 364. Diagrammatic cross-section of the spinal cord with dorsal and ventral roots of the spinal nerves. (After Adams, *An Introduction to the Vertebrates*, John Wiley & Sons.)

tral roots of the spinal nerves and into the autonomic ganglia, where they make synaptic connections with neurons (post-ganglionic) that send axons on to the visceral effectors. Afferent autonomic nerve cells may connect in the spinal cord with the same association neurons as sensory nerve cells from the outer body regions entering at the same level of the cord. Hence pain impulses reaching the cortex are sometimes interpreted not as coming from the viscera but from those body parts served by sensory neurons of the same level. For example, pain arising from irritation of the stomach may cause tenderness of the skin over the tip of the breastbone. Such translocation is called *referred pain*.

One of the outstanding functions of the autonomic system is the unconscious adjustment of the organism to fluctuating functional demands of the body. In a state of emergency, initiated by anger, fear, or other excitement, the body is organized for conflict or flight. Blood is rushed from the viscera and skin to the skeletal muscles. Digestion is inhibited, the skin pales, and an abundance of sugar is poured into the blood from the liver and directed to the skeletal muscles in preparation for violent

action. The heart beats faster, blood pressure rises, and the intestine and bladder may even be emptied. These effects are attributed to *sympathin*, a substance liberated at the nerve-endings of the sympathetic system. Sympathin is similar in its effect to the hormone adrenalin, which is secreted by the adrenal gland of the endocrine system. Moreover, stimulation of the adrenal gland by branches of the sympathetic nervous system causes the secretion of adrenalin which, circulated through the bloodstream, augments these responses. Thus the two systems of nervous and endocrine coordination work very closely together. Another substance (*acetylcholine*), having an effect opposite to that of sympathin, is released by the parasympathetic system.

There appears to be an even greater affinity between the two systems, for widely scattered cells within the autonomic systems of both vertebrates and invertebrates show both nervous and glandular structural features. In arthropods these appear to be associated with developmental processes, which these cells control through their secretions.

Autonomic functions are served by various regions of the spinal cord and brain, and all appear to be under ultimate domination of the cerebral cortex. The simplest autonomic reflexes are at the spinal level. Thus, regions of the body served by a part of the spinal cord which has been severed from the main system still show various reflexes, such as sweating, changes in blood pressure, and emptying of bladder or rectum. If the system is severed above the medulla, more highly organized autonomic integration remains: heat regulation is improved, although it is still below par, and the organism can cough, sneeze, swallow, and salivate. Other autonomic reflexes of a higher order are centered in the hypothalamus, a ventral region of the posterior division of the forebrain, and indeed, this appears to be the main governing center of the autonomic system, both sympathetic and parasympathetic. Here are integrated many phases of metabolic activity, such as regulation of heat loss or heat conservation through such devices as sweating,

panting, erection of hair, and dilation or constriction of blood vessels. The hypothalamus in turn is regulated by the cerebral cortex. Hence by dint of concentration and "will power," it is possible to exercise some degree of conscious control over certain of the so-called autonomic reactions.

The autonomic nervous system coordinates internal body activities without burdening consciousness with them. It is autonomic in this sense. Otherwise, it is no more independent than the circuits which cause automatic reflexes.

THE ENDOCRINE SYSTEM

The realization that glands within the body produce coordinating substances dawned upon clinicians and physiologists gradually and surprisingly recently, although some vague knowledge of them dates back to antiquity. Galen, in the year 200 A.D., knew of the pituitary gland, and diabetes was described as far back as 500 B.C., but without knowledge of function or cause in either case. The effects of castration — man into eunuch, bull into ox — were well known to the ancients.

History of Endocrinology

When in 1858 a Geneva physician removed the thyroid gland of a dog, with a fatal result, and so demonstrated its importance, a new interest slowly awakened, and medical men and research workers in many countries contributed clinical observations and the results of their experiments on animals. Before 1900, a peculiarly enervating disease, *myxedema*, had been shown to be associated with atrophy of the thyroid gland. Later some patients with myxedema had been fed thyroid extract and their condition improved. It had also been found that removal of the pancreas of a dog resulted in severe and fatal diabetes. At the turn of the century, an American pathologist discovered that certain structural parts of the pancreas of defunct diabetics had degenerated beyond recognition. The Russian Pavlov had observed that stimulation of the intestine with acid caused pancreatic secretion. In 1901 the

Japanese Takamine isolated an active substance, *adrenalin*, from the *adrenal glands*, which some years previously had been found to cause a marked rise in blood pressure. The next year, Bayliss and Starling, two British physiologists, found that acid causes the duodenum, even when it has been severed from all its nerve connections, to secrete a special substance that passes into the blood and causes pancreatic secretion. They called the substance *secretin* and adopted the name *hormone* (Gr. *hormaein* = to arouse) for such substances in general. In 1922 the young Canadians Banting and Best confirmed the theory that the pancreas produces an internal secretion which controls sugar metabolism and became the discoverers of *insulin*. These are but a few of the contributions that first trickled and then streamed into scientific journals on this one subject of the endocrines, but they serve to demonstrate the international character of science. Endocrinology has grown enormously even in the last few years, and holds untold promise for the future.

Importance of Hormones

The endocrine system, while closely associated with the nervous system, is not so closely knit. It consists of various isolated ductless glands which secrete hormones into the blood stream. These glands appear to have evolved rather late in the evolutionary process — later than the nervous system — for definite endocrine glands are known only in the arthropods and the chordates. But specific chemical substances known to act as coordinators are well known as embryonic determiners and differentiating substances, and the auxins of plants. These do not differ basically from hormones, and thus the fact that no specific endocrine glands have been found in lower metazoans does not mean that they have no hormonal coordination.

Specific endocrine glands — often derived from nervous structures — have been found in arachnids, crustaceans, and insects, and the minute size and specificity of some of these are no less striking than the complexity of their

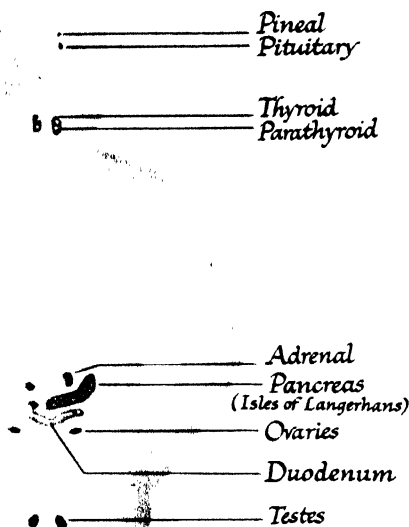


Fig. 365. The endocrine glands in the human body.

interactions. In arthropods, hormones control such processes as growth, molting, differentiation, and metamorphosis.

In vertebrates the endocrine system consists essentially of seven glands or groups of glands, the *pituitary*, *thyroid*, *parathyroid*, *duodenum*, and *adrenal* glands, and the *pancreas* and *gonads*. Several of these glands are compound in structure and origin, and a single gland may produce a number of diverse hormones. For example, several different hormones influence the growth of the gonads. Also, some of these glands, besides being endocrine, secrete other products into ducts. There are no doubt more hormones still to be discovered, and perhaps additional endocrine glands will be added to the list.

Hormone Effects

Apart from the striking diversity of hormone effects, their evolutionary significance lies in their universality among vertebrates. Indeed, the same hormones characteristically produce corresponding effects in all vertebrates. On the other hand, certain hormones which are found in widely varying animal groups do have

specific effects in one but not in another. Thus in fishes, amphibians, and some reptiles, hormones control the color and expansion of pigment cells (chromatophores), which cause striking changes in skin color. Although birds and mammals no longer have chromatophores, many still retain these same hormones. Similarly, although milk is produced only by mammals, "milk-forming" hormones are found in all vertebrate classes, suggesting that these hormones were drafted for their new use and previously served another.

Some of the clearest effects of hormone activity appear in the control of sex structures and behavior. During the pre-mating period, normal male frogs develop calluses on their thumbs, and the musculature of the fore limbs becomes strengthened in preparation for the clasping of the mate in copulation. When the mating period arrives, the male exhibits a marked behavior pattern composed of a series of necessary reflex activities. But if the testes are removed, none of these things will occur. If tissue from the testes is now transplanted beneath the skin of such a castrated frog, even without any direct contact with the circulatory or nervous systems, normal sexual structures and behavior will reappear. Thus it is evident that one or more hormones secreted by the testes act as an essential activating agent. This continues to be secreted so long as the tissue remains alive.

Even the embryo within the uterus produces hormones capable of influencing the physiological condition of the mother. Tissue taken from the milk gland of one guinea pig and transplanted under the skin of the ear of another, pregnant guinea pig will begin to secrete milk when the host gives birth to her litter, reacting exactly like her own milk-gland tissue. Since milk glands can be similarly stimulated by the injection of embryonic extracts, while uterine or placental extracts have no such effect, we may conclude that the embryo contributes hormones inducing lactation.

The function of hormones in coordinating the normal secretion of digestive glands has been brilliantly demonstrated in various ways. By

cross-joining the circulatory systems of two dogs so that the blood of each must flow through the body of the other, it has been shown that substances coordinating digestion are transmitted by the blood stream. In normal dogs, food passing into the intestine causes secretion of the pancreas. In the dogs with joined circulations, feeding one causes pancreatic secretion in both. Since the circulating blood is the only contact between the two dogs, the presence of a hormone which stimulates the pancreas was thus confirmed.

Hormonal control of body activities is widespread and many tissues contain endocrine structures, although most is known about the seven special endocrine glands of man.

Thyroid

The thyroids lie on either side of the larynx, and in man are united into a single gland. The active part of the thyroid hormone, *thyroxin*, controls the level of the basal metabolism, involving such functions as oxygen consumption, the rate of formation of nitrogenous wastes, irritability, and the desire for sleep. An extreme deficiency of thyroxin in early childhood causes *cretinism*, a special type of dwarfing and idiocy. A deficiency occurring later on, in puberty and afterwards, retards sexual development and causes mental lethargy, an accumulation of fat, and the peculiar flabbiness of features that accompanies myxedema (Fig. 366). Excessive thyroid action has nearly opposite effects — irritability, emaciation, dryness of skin, and adrenal insufficiency, coupled with a peculiar pop-eyed condition called *exophthalmia* (Fig. 367). Since iodine is a necessary component of thyroxin, any lack of iodine in the diet causes a compensatory over-development of the thyroid gland. This produces a neck swelling known as goiter. Small quantities of iodine in the diet will alleviate simple goiter. Roger of Palermo, famous physician and alchemist, in 1180 prescribed ashes of sponges and seaweed for goiter, and a full thousand years earlier, the ancient Greeks had prescribed the drinking of sea water for goiter. The Chinese in ancient times also recommended

seaweed. Since these prescriptions contain iodine, they may indeed have been effective.

Fig. 366. Myxedema, a condition caused by thyroid deficiency in adults. Before (above) and after treatment.

From the Thyroid Clinic of the Massachusetts General Hospital

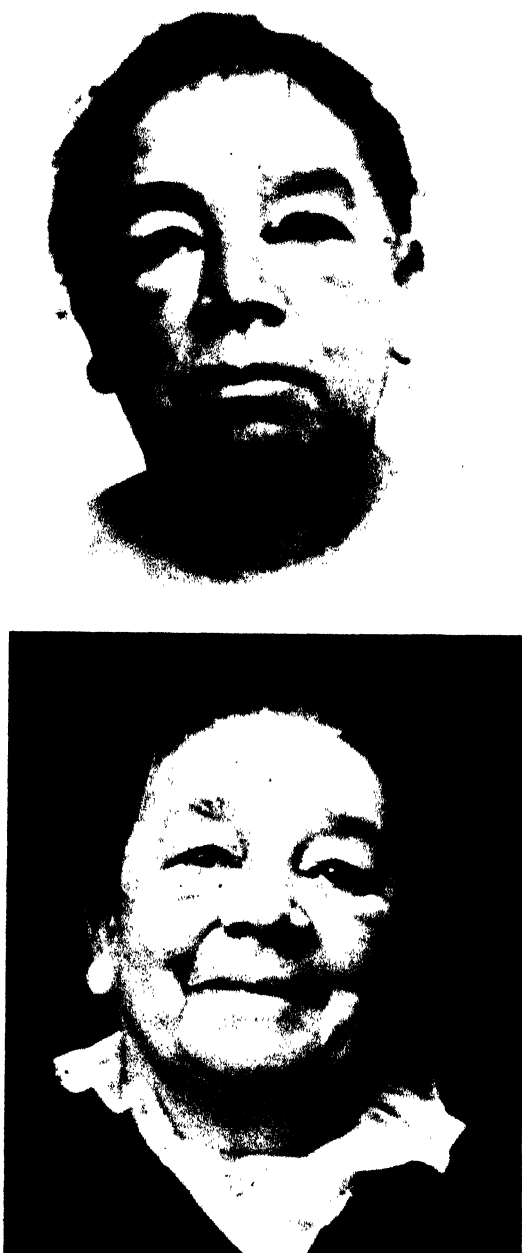




Fig. 367. Hyperthyroidism, produced by over-activity of the thyroid gland.

From the Thyroid Clinic of the Massachusetts General Hospital

Parathyroid

Imbedded in the tissues of the thyroid are two pairs of minute glands, the *parathyroids*, which produce the hormone *parathormone*. As they were not discovered until 1891, because of their size and position, ignorance of the existence of these glands caused much confusion concerning the activity of the thyroids before that date. For fatal effects follow removal of the tiny parathyroids, but a major portion of the thyroid gland itself can be removed without any such drastic result. Parathormone plays an important role in maintaining the calcium level in the blood. Over-production raises the amount of calcium in the blood at the expense of the bones, which consequently become pliable and grotesquely and painfully twisted. A deficiency of the hormone causes a marked increase in irritability as a result of the drop in blood-calcium, followed by involuntary muscle spasms, convulsions, and finally death.

Adrenals

On the upper curve of each kidney is a cap-shaped adrenal gland about the size of a small potato. These were discovered by Eustachius in 1663, but their function long remained a mystery. Even a prize offered by a scientific academy in the eighteenth century brought no solution, although many suggestions were made — among them, that they served as bumpers to keep the stomach from resting too heavily on the kidneys!

Despite its minute size, each adrenal gland consists of two parts, each producing different hormones. The innermost part, or medulla, produces the well-popularized *adrenalin*, discovered in 1894 and independently produced in pure crystalline form by Takamine and by Aldrich in 1901. This hormone has numerous effects, such as causing the spleen to release more red blood cells into the circulation, causing the liver to increase the blood-sugar level, and constricting visceral blood vessels and dilating those in the skeletal muscles. Thus adrenalin is an emergency hormone, preparing the body for fight or flight. Its action is associated with the emotions of fear and anger.

The outer layer, or cortex, of the adrenal gland produces a number of chemically similar steroid hormones. Some of these are *androgens* (Gr. *aner* = man + *genes* = born), like the sex hormone of the testis, *testosterone*, or *estrogens* (Gr. *oestros* = gadfly > frenzy + *gen*), like the sex hormones of the ovary. These assist in maintaining the secondary sexual characteristics. The rate of production can be conveniently measured in terms of the rate of excretion, and we find that a normal 20-year-old male excretes about 16.6 mg. in 24 hours, compared to 11.5 mg. in the female. If the production in a female rises to the male level, male characteristics develop (bearded women, etc.) and perhaps vice versa.

Certain of the steroid hormones are involved in sugar metabolism. Among other functions, they regulate the transformation of proteins into carbohydrate and also indirectly affect the balance of water in the body by controlling

the excretion of sodium salts by the kidneys. In opposition to the effect of parathormone deficiency, a deficiency of these hormones causes decreased excitability, to the point of coma and even death.

Pancreas

Almost everyone has heard of diabetes and of insulin, perhaps because the disease is still only too common. It is by no means a new disease, for it was described as early as 500 B.C. in an Egyptian papyrus. But what causes diabetes was not discovered until well over two thousand years later. Although its relation to the pancreas was known by 1900, the hormone it produces, insulin, was not extracted until 1922. Shortly thereafter the hormone was produced in sufficiently pure form to be non-irritating and suitable for treatment of diabetics.

The pancreatic tissues that produce insulin are distinct from those producing the pancreatic enzymes and are microscopically visible as definite islands, called the *islands of Langerhans* — whence the name insulin (*insula* = island). Insulin appears to be essential for cells to burn and store sugar. Lack of sufficient insulin results in starvation in the midst of plenty — the cells starve for sugar, while the blood-sugar level rises. The excess sugar filtered through the kidney is not reabsorbed, and sugar remains in the urine to be excreted. The general effects may lead to death.

Gonads

The gonads of the two sexes produce similar but not identical hormones. The principal male hormone, *testosterone*, is produced by cells located in between the testis tubules, which produce the sperm cells. It has both physical and psychic effects. At puberty, it acts to increase the size of the penis, to aid in the ripening of sperm cells, and to intensify sexual drive. It aids in bone and muscle growth after puberty, and together with the adrenal androgens it produces male hairiness, rougher skin, and other effects. *Estrone*, a female sex-hormone, produced by the same follicles of the ovary in which the egg cells develop and mature, is

analogous to testosterone. Both of these sex-hormones have powerful psychological effects, and since they are the basis for normal sexual development, they play a decisive role in human behavior.

Hormones in the Female Sexual Cycle

One of the most interesting and most involved examples of reciprocal hormonal control is in the female sexual cycles of menstruation and pregnancy. Numerous endocrine glands and tissues with endocrine functions are involved in this, among them the pituitary gland, the ovaries, the embryonic placenta, the adrenals, and the thyroid glands (Fig. 368). The full and exact interrelationships of these glands is far from clear.

In mammals ovulation occurs at specific intervals, sometimes seasonal. Tiny hollow spheres of cells in the ovaries, called follicles, burst, one or several at a time depending on the species, enlarge to the size of a pea, and discharge a ripe egg each. Such an egg, if it is not fertilized by a sperm cell within the ensuing ten to twelve hours, disintegrates. In most mammals fertilization at the proper moment is favored by a correlated physiological and psychological change in the female, causing her, through her actions and otherwise, to become sexually attractive to the male, and for the time receptive to his attentions. This is often accompanied by vaginal swelling and discharge. The animal is then said to be in *estrus* or "heat," and only at this time will she willingly mate.

In man and some primates there is no estrous cycle but there is a *menstrual cycle*, also with periodic discharges, though uterine rather than vaginal in origin. Estrus occurs at the time of ovulation, whereas the primate's menstrual flow appears to occur at a period about midway between ovulations. Correspondingly, changes in behavior, like those in the estrous female, appear to be slight or absent in primates. There may be a hint of psychological change corresponding to estrus at the time of ovulation. But while individuals experience fluctuations in sexual inclinations, the correlation of

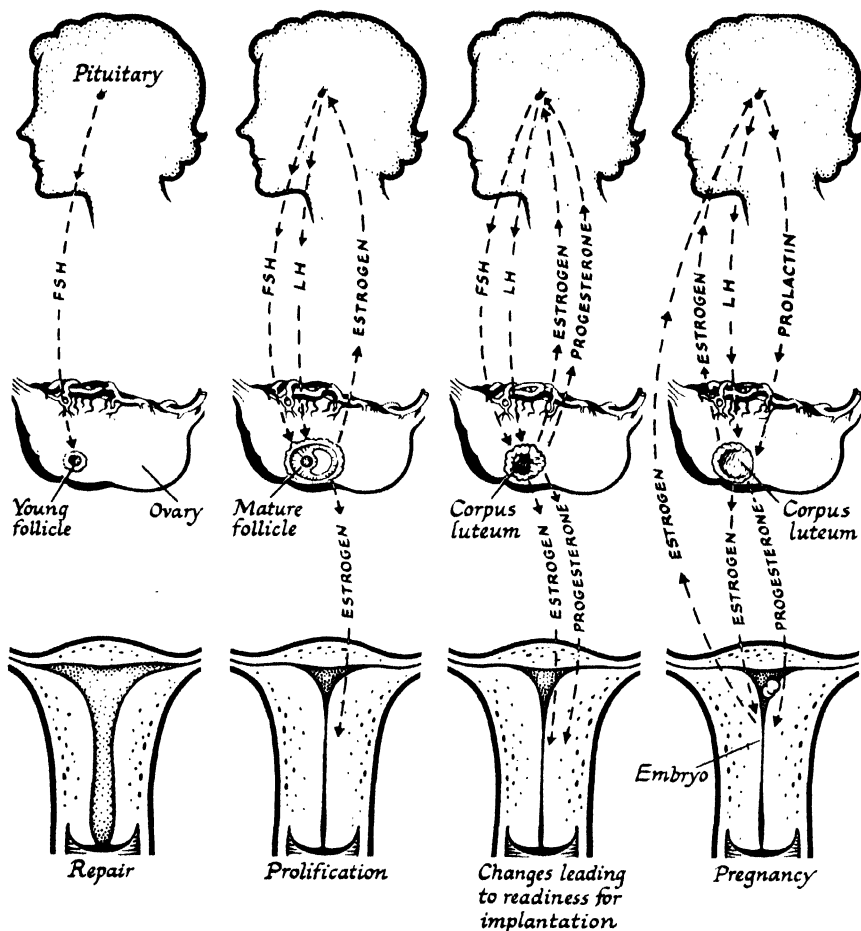


Fig. 368. Hormonal relationships in the female sexual cycle.

these with the menstrual cycle seems quite variable.

In the human female, the menstrual cycle begins about every twenty-eighth day, though the period may vary normally between twenty and thirty-five days. The uterine lining increases in thickness and vascularity, individual blood vessels swell and burst, and some of the uterine epithelium sloughs off with more or less hemorrhage, producing the menstrual flow. Thereafter a period of repair and growth ensues, reaching its climax again at ovulation. If the ovum is fertilized, the uterine wall continues to proliferate and maintains its vascular structure. If not, it again disintegrates in menstruation. How does the uterus "know" when to prepare for a fertilized ovum, and, if the expected guest fails to appear, what signals

the uterus to regress and start its preparation all over again?

Simplifying and omitting many still controversial relationships, we may summarize the main features of the control of the menstrual and pregnancy cycles as follows. The anterior lobe of the pituitary gland produces a follicle-stimulating hormone (FSH for short). This, secreted into the blood stream and carried by it, has the action its name implies. Under its influence, the follicle grows, and as it does, produces one or more steroid hormones called *estrogens*. These exert effects in two directions, one on the lining of the uterus which prepares it for the implantation of an egg, should this become fertilized. The other action, on the pituitary, leads to the gradual inhibition of FSH production and its replacement by a second

anterior pituitary hormone, the luteinizing hormone (LH for short). Eventually the ripe follicle in the ovary bursts, liberating a mature ovum. The ruptured follicle, under the influence of the LH, now becomes filled with yellow gland cells, making the *corpus luteum*. This produces still another steroid hormone, *progesterone*, which completes the preparation of the uterus for the implantation of the fertilized egg and, in case this occurs, is necessary for the formation of the placenta. Meanwhile, with the rupture of the follicle, the production of estrogens declines. This tends to reverse the action of the anterior pituitary gland again, switching it from the manufacture of LH to FSH. So, if the egg is not fertilized and implanted, the corpus luteum will begin to shrink and degenerate and the menstrual breakdown and discharge of the uterine lining will follow. The menstrual cycle begins again.

But if the egg is fertilized and implanted, the developing embryo and the growing placenta form estrogens which act on the anterior pituitary, make it keep up the production of LH, and so in turn prevent the corpus luteum from degenerating and the menstrual changes in the uterus from occurring. For the first four or five months of pregnancy this mechanism is necessary to prevent miscarriage. The corpus luteum grows to an enormous size, in fact, during this period. But later it begins to decline and progesterone no longer seems to be needed to maintain the placenta. In this latter part of pregnancy, the anterior pituitary also produces another remarkable hormone, known as *prolactin*, which initiates the development of active milk glands in the breasts and eventually stimulates the production of milk. This hormone also has considerable influence upon behavior, appearing to be responsible in mammals (and in pigeons as well), for the mothering instinct which, in the absence of own young, will sometimes lead to the strangest adoptions. Mother cats will even adopt infant rats; and pigeons will brood on smooth stones in lieu of eggs.

It must be noted that these are not the only hormones or endocrine glands involved, or

the only changes that occur. Furthermore, the time, the quantity, and the interrelations with other hormones have a decisive bearing on the action which any given hormone will have. Thus, LH is unable to produce its characteristic effects if FSH has not prepared the way. And an excess of estrogens may inhibit release of prolactin, and so inhibit the production of milk after it has already started. On the other hand, a continued supply of estrogen is instrumental in building up the milk glands; while the withdrawal of ovarian and placental estrogens and of progesterone before and especially at the time of birth, causes the increased release of prolactin from the pituitary that actually initiates lactation. All in all, no other cycle can better illustrate the extreme complexity and delicate interplay of hormones in controlling body functions.

Pituitary

This master gland coordinates the activities of many others. The effects of this small body at the base of the brain are so widespread and so vital to normal functions that a person deprived of it would be incapable of long survival. Not much larger than a pea, the pituitary yet has a dual role and origin. Its anterior portion, formed from the roof of the mouth during embryonic growth, comes from the epithelium. The posterior lobe is a specialized extension of the brain, to which it remains attached.

The anterior lobe produces no less than six known hormones and perhaps as many as five others. One hormone influences the activity of the thyroid, and enables its cells to produce thyroxine. Another is a growth hormone, failure of which is responsible for perfectly formed midgets, unlike cretins, of normal intelligence. Excess of this hormone in early life, on the other hand, causes gigantism. A pituitary tumor may cause excessive activity in adults, so that chin, nose, ears, hands, and feet continue to grow, resulting in the characteristic distortion of features known as *acromegaly*. Normally production of the growth hormone diminishes at puberty, and the anterior lobe shifts to the production of hormones which

affect the gonads and their increased production of testosterone in the male and of estrone and progesterone in the female, which in turn influence the termination of growth. These pituitary hormones also have a direct effect on the production of mature sperm and on the cycle of ovulation. There is also a pituitary hormone which influences the production of the steroid hormones in the cortex of the adrenal glands, and there is also one, called *prolactin*, which stimulates the mammary glands to produce milk. This hormone is so potent that injections of it will even cause virgin females to secrete milk. It appears to have a lot to do with the "mother instinct." It makes birds brood, even without eggs to sit on.

The posterior pituitary lobe is richly innervated and connected with the brain. So far as is known, its primary action is the production of a hormone which controls the balance of water in the body. Over-production of the hormone results in excess water storage in body tissues. Lack causes excessive water elimination and thirst. Another action of extracts from this part of the gland, due to a separate hormone, is greatly to increase the contraction of smooth muscle. This effect is specially marked in the uterus, and assists in giving birth to the young.

Vital as are the effects of the hormones, they would be wholly ineffectual but for the special ability of certain tissues to respond to them, for it is only through these that they act. They are to be considered no more than a special part of the environment of a tissue, produced, however, by other tissues of the body. Though testosterone stimulates the growth of hair on the face, this will not develop if the genes for

hair growth are not present. Eunuchs treated with testosterone will develop masculine characteristics such as masculine musculature, if it lies within their genetic makeup to do so. But no amount of testosterone will make a Hercules out of a genetic weakling.

The endocrine glands are delicately adjusted to each other and are of vital importance in coordinating some of the most complex activities of growth and metabolism. They are indispensable in welding an integrated unit out of a vast mass of otherwise largely disconnected tissues.

THE VERTEBRATE SKIN

The slow evolution of the vertebrate skin may be traced by studying the lower vertebrates of today and the embryological development of the higher ones. The skin of the higher vertebrate is a combination of ectodermal and mesodermal structures. Originally it was formed by a single layer of living outer cells. As organisms increased in size, and later as they began to leave the water, forms with a rapidly proliferating skin proved to have a better chance of survival, so that the skin became stratified, with increasing layers of dead cell bodies forming an outer protective coat. Supporting these conclusions is the fact that in early stages the skin of the human embryo consists of a single sheet of cuboid cells. Later, non-specialized mesenchyme cells differentiate to sensitize, nourish, and support the epidermis, and thus an inner layer, the dermis, is formed.

In mammals, the skin (Fig. 369) reaches the greatest degree of complexity and versatility. In human skin, the epidermis consists of four layers — the bottom germinative layer of liv-

Fig. 369. The human skin in cross-section (model).



ing and constantly reproducing cells, and three outer layers of cells in successive stages of cutinization and compacting. These dead cells form a tough yet flexible protection against such dangers as desiccation, light, heat, mechanical injury, chemicals, and attacking organisms. The outer horny layer constantly flakes off removing stain and grime, while new millions of cells daily replace what is lost.

The dermis consists entirely of living cells. Its upper surface, upon which the germinative layer of the epidermis rests, is in the form of finger-like projections, or *papillae*. These greatly increase the contact surface between the two layers, so that nutrients pass readily from the richly suffused capillaries of the papillae to the living cells of the germinative layer, which have no other supply of food. Below the papillary layer lies a network of fibrous tissue, within the spaces of which lie fat deposits and sweat glands. Both these layers contain many free nerve endings, as well as specialized sense organs, such as the tactile corpuscles and the receptors of deeper pressure. Both layers also contain networks of blood and lymph vessels. Here in the dermis lie the infolded epidermal pockets, or follicles, which produce hairs, together with sebaceous and sweat glands.

In the earliest stages of vertebrate evolution, heavy bony armor in the dermis was common. In recent vertebrates, less cumbersome reinforcements have evolved, such as scales, feathers, hair, and also teeth, nails, claws, and hoofs.

Fishes and amphibians still have a delicate non-cellular cuticle as a protection over the glandular epidermis, but in land vertebrates, the outer epidermal cells become transformed into horny scales and serve as a tough protective layer. The beginnings of this process are evident in the fishes, but it becomes pronounced only in land animals. The scales of bony fishes are formed from the dermis and grow beneath the soft glandular epidermis. In the cartilaginous fishes, however, the epidermis itself produces the tooth-like placoid scales, from which our own teeth appear to have been derived.

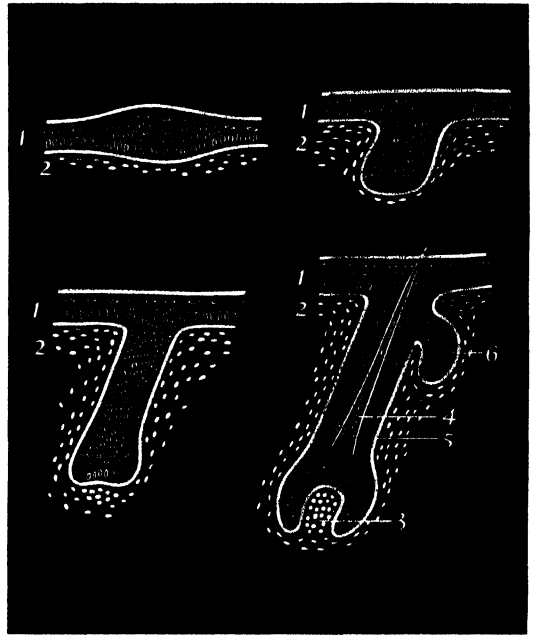


Fig. 370. Diagram illustrating development of hair. Diagrams of hair-sections at different ages. 1. Epidermis. 2. Dermis. 3. Hair papilla. 4. Young hair. 5. Sheath. 6. Sebaceous gland.

Scales of reptiles are largely products of the dermis, with no bone core, but with an external coat of epidermal enamel. Feathers are glorified reptilian scales, almost wholly epidermal in origin (Fig. 371). Mammalian hairs are of uncertain evolutionary origin, but embryologically their structure is wholly epidermal (Fig. 370). A hair is merely a specialized epidermal thread, grown in a follicle which dips down into the dermis. Like feathers, hairs have a limited life span, at the end of which they drop out, to be replaced by new hairs, grown either in a new or in an old but rejuvenated hair follicle.

Functions of the Skin

From fish to man, the skin serves many functions. It covers and protects against mechanical injury. It conserves the salty liquid environment of the tissues, and in lower aquatic vertebrates assists in respiration. The skin of land vertebrates keeps them from drying out. It prevents invasion and infection by bacteria

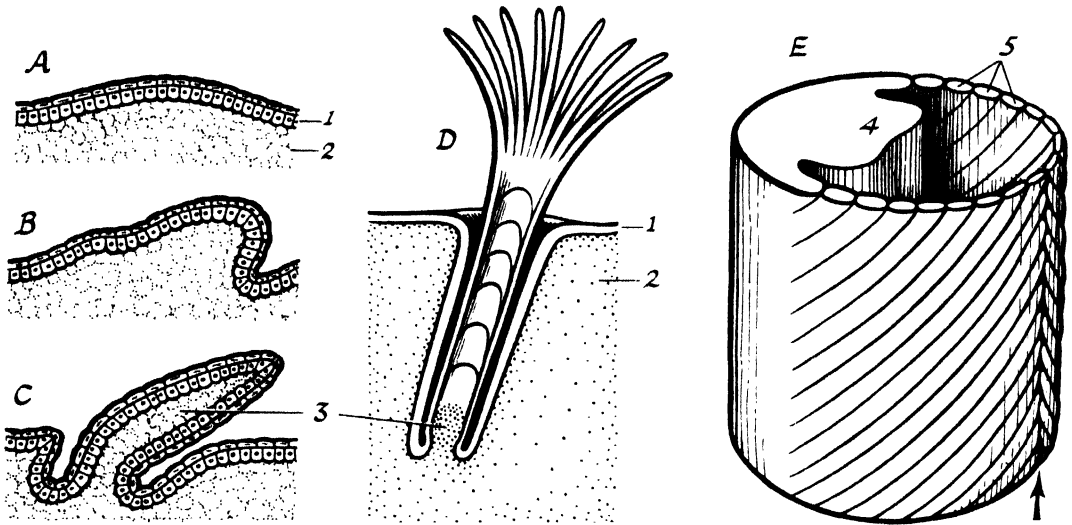


Fig. 371. Diagram illustrating development of feathers. *A-C.* Median sections through feather buds of various ages. *D.* Down-feather, sectioned. 1. Epidermis. 2. Dermis. 3. Feather papilla. *E.* Differentiation of epidermal tube during development of feather. 4. The shaft. 5. The remaining wall splits into diagonal sections which later split along the line of the arrow, fold back, and become the barbules of the vane.

and other agents, as we may discover if a cut or abrasion is neglected. Numerous sensory structures are imbedded below its surface, so as to inform the organism of heat, cold, pressure, injurious agents, and other phenomena. It screens out radiations injurious to living cells, and pigment cells further aid in providing protective coloration, which in cold-blooded animals may even change in response to altered environmental conditions. In these lower vertebrates, mucous glands lubricate and protect the skin against drying out, while in higher vertebrates, oil or sebaceous glands lubricate the skin and keep it pliable. Skin derivatives, such as scales, feathers, and hair, serve as protectors against mechanical injury, and in some land animals against temperature fluctuations. Other skin derivatives of more localized use are nails, claws, hoofs, and horns. Even those astonishing food-producing structures, the mammary glands, are skin derivatives, for they are modifications of those mammalian heat regulatory and secretory structures, the sweat glands. It is noteworthy that the billions of densely packed dead cells in the outer horny layer of the skin are all expendable, and are

sacrificed for the good of the organism as a whole. No single cell wall, however thick, could stand up under the mechanical abuse sustained by the skin of a large vertebrate.

Glands in the skin serve several functions. In fishes, mucous glands lubricate and protect against parasites. In amphibians, similar glands produce moisture-holding films, while specialized glands may produce protective, acrid, or poisonous secretions. In most reptiles, and in some birds too, skin glands play a minor role, though in many mammals they are vital. Sebaceous glands lubricate and oil; sweat glands excrete and, by evaporation, cool; and in many animals the odors they give off serve in sexual notification or stimulation.

Sense Organs in the Skin. The sensitivity of the skin is the combined effect of specialized receptors. Pain is probably recorded by free nerve endings, but pressure, traction, cold, heat, tickling sensations, and others are recorded through special, separate sense organs (Fig. 369). The skin is by no means uniformly sensitive to these various stimuli, but is a mosaic of receptors. Thus regions devoid of specific receptors are unable to respond to cor-

responding stimuli. Pain, which most of us think no blessing, and usually strive to eliminate, is a sense of vital importance, for it calls attention to abused or damaged regions, prompting the organism to avoid further damage and to be cautious in the use of such structures so that tissue repair may proceed undisturbed. The significance of such warning devices to the survival of the organism becomes apparent when we observe what happens to the occasional human being unable to feel pain. Such children have been known to place their hands on hot stoves, laughing while their flesh seared. Insensitivity to pain does not, of course, exempt them from danger to infection and consequent danger to life.

Heat Regulation

Heat regulation in birds and mammals is largely effected through changes induced in the skin. Hair and feathers enclose dead air spaces, preventing heat loss. This space may be varied by erecting or flattening the hair or feathers. Small muscles at the bases of the hairs function in most mammals, in response to lowered temperature, by erecting the hairs

and so increasing their insulating effect. These are still functional in man, but having far too few hairs to be effective, we succeed only in getting "goose pimples." In conjunction with this reaction, the distribution of blood to the skin capillaries regulates the amount of heat lost. The diameter of these vessels is under the coordinating influence of the autonomic nervous system. In many mammals sweat glands, controlled by a heat-regulating nervous center in the brain (Thalamus), are used as an added efficient temperature control. Rise in temperature stimulates sweating, which cools by evaporation. Falling temperature, conversely, reduces sweating.

In the evolution of the skin, we glimpse once more the power of random mutation and selection in producing an effective instrument for the most diverse needs, from the simple epidermis of *Amphioxus* to the sheath of armored dinosaurs and the complex regulatory skins of birds and mammals, with their feathers or hair, protective qualities and special devices for excretion and heat regulation, as well as wings, claws, hoofs, horns, and even the food-producing milk glands.

The Vertebrate Pattern: Principal Organ Systems

THE DIGESTIVE SYSTEM

In the vertebrates, as in the higher invertebrates, the parts of the originally simple digestive tube are differentiated into specialized structures for ingestion, digestion, and absorption. Thus the vertebrate digestive canal is divided into an oral cavity, a gullet or esophagus, a stomach, and an intestine. In addition, all vertebrates possess important glandular intestinal outgrowths, the liver and the pancreas (Fig. 372). The digestive tracts of different vertebrates are all mere variations of this plan, though from class to class up the evolutionary tree, we find increasing efficiency in general, and a great variety of specialization for the handling of different types of food and of food-getting.

The Basic Plan

Except in the cyclostomes, the vertebrate mouth usually has jaws and teeth or beak-like substitutes for teeth. There may also be lips, a variously modified tongue, and glands in the mouth producing digestive enzymes. The mouth, with its accessory structures, shows a greater variety of adaptations of form than probably any other part of the body.

A food-pipe or *esophagus* connects the mouth with the main body of the tract, and usually leads into an expanded sac-like structure for temporary storage and digestion, the stomach, which is generally equipped with digestive glands that secrete protein hydrolyzing enzymes. Among fishes, some species have a stomach-like enlargement of the digestive tube which is not glandular; others have a glandular structure which is not enlarged, and may be

classed as a stomach only because of its position. Other vertebrates show all gradations from the non-glandular to the wholly glandular stomach, depending on the type of food eaten. In the toothless birds, and in some reptiles, the stomach has been converted into an enormously muscular grinding organ, the *gizzard*, where food is mechanically reduced with the aid of included pebbles or grains of sand.

From the stomach, the food passes into the *intestine*, where the main digestive and absorptive activity takes place. The intestine is usually separated from the stomach by a distinct change in structure and by a muscular sphincter, the *pylorus*. Although the intestine is itself glandular, its digestive fluids are fortified by enzyme-bearing fluids and other agents secreted by the pancreas and the liver. Pancreatic fluid contains enzymes capable of hydrolyzing all three food classes, carbohydrates, proteins, and fats. The liver secretes a fluid, the bile juice, which may be temporarily stored in a sac, the *gall bladder*, or may flow directly into the intestine. Bile juice contains products of red blood cell disintegration and bile salts, which aid in saponifying and emulsifying fats, thus maintaining them in a state of fine division which enhances enzyme action. Numerous other functions of the liver in preparing and storing absorbed foods will be discussed in Chapter 23. Intestinal fluids, produced by the *intestinal glands* in its walls, contain enzymes which continue and complete the hydrolytic action. Digestible foods are thus reduced to a soluble form and diffuse through the tissues of the intestine into its capillary blood-vessels or into its lymph vessels, which eventually enter the circulation.

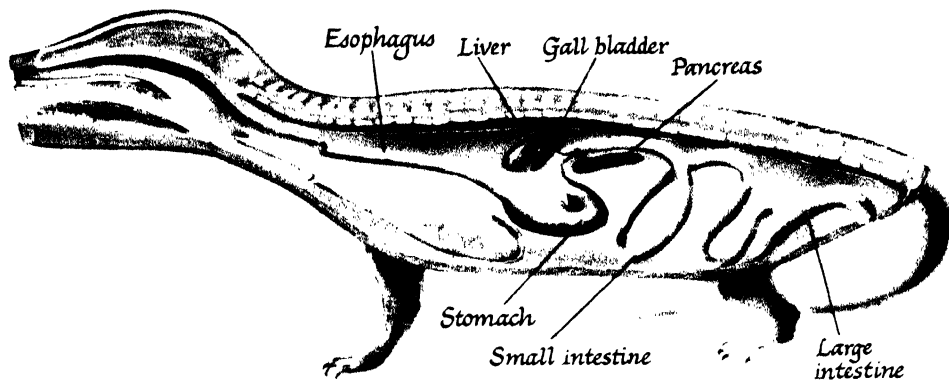


Fig. 372. Generalized plan of the vertebrate digestive system.

The effective absorbing surface of the intestine is increased in a variety of ways. In some vertebrates the tube is long and thin; in others, short and thick. In still others, the surface is increased without increasing its length or diameter, by folds, ridges, or projections of the inner wall. In most vertebrates, the intestine is differentiated into the *small intestine*, which leads from the stomach, and its continuation, the *large intestine*. The latter contains no digestive glands, but may be rich in mucus-secreting glands. Here occurs further absorption, and in higher vertebrates especially the reabsorption of water.

Origins and Development

The vertebrate digestive cavity is a direct descendant of the coelenterate type of gastro-vascular cavity. In the vertebrate embryo, after invagination or ingrowth of the blastula or its counterpart, a double-walled cup, the *gastrula*, is formed. In higher vertebrates with rich yolk endowment in the egg, this process is often modified almost beyond recognition, but the basic principle remains much the same. The original mouth of the gastrula, the *blastopore*, is soon obliterated, after serving briefly as a connection between the neural canal and the hind-gut, while a new mouth, remote from the original mouth of the gastrula, is formed. A new posterior opening, the anus, is established later, in the vicinity of the primitive mouth (Fig. 373). The endodermal primitive gut thus formed gives rise only to the ultimate

lining of the permanent digestive tube, to the secretory parts of the digestive glands, and to the respiratory tract, while mesodermal tissue soon becomes applied to the endoderm and produces the main bulk of the digestive organs. The anterior and posterior ends of the digestive tube are produced as infoldings of ectoderm, giving rise to such structures as the salivary glands and the outer coating of enamel on the teeth. The rest of the digestive tube has much the same structure throughout: there are four main tissue layers, the mucous, the submucous, the muscular, and the serous (Fig. 375). Thus the actively secreting and absorbing tissue, the mucous layer, is endodermal in origin, but the supplying and muscular components are mesodermal.

The exposed inner surface of the intestine is folded or drawn into finger-like projections, the *villi*, each with a submucous center. Many pits or depressions in the surface, produced by infoldings of the epithelial lining, are the glands. These vary in structure and function, some secreting digestive enzymes, others acid, and still others mucin, or combinations of these. The submucous layer consists of loose connective tissue, blood vessels, and nerves, which supply the overlying mucosa. The muscular coat typically consists of two layers, an outer one of longitudinal fibers and an inner, thicker one, of circular fibers. The latter constricts and thus churns and by wave-like movement of the constriction along the digestive tube propels the food mass. This is called *peristalsis*.

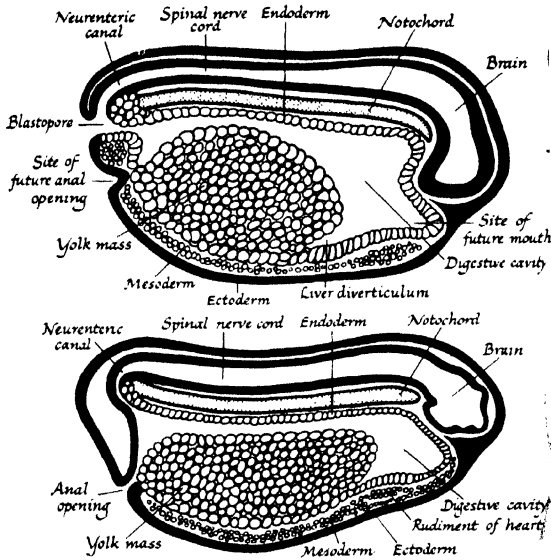


Fig. 373. Median sagittal section of frog embryos. (Kellicot, after Marshall.)

In the stomach there is a third diagonal muscular layer, which increases its power. The outer or serous layer of the intestine forms a thin smooth coating over the entire tract. It is similar to and continuous with the inner lining of the body cavity, the *peritoneum*. Picture a length of garden hose suspended inside a stove pipe by means of a thin sheet of rubber, the sheet cemented smoothly to the entire inner surface of the pipe except at the top, where a loose fold hangs down to its center. In the cradle thus formed, the hose lies suspended.

Thus the hose is supported by a double thickness of the same tissue that lines the pipe and also covers the surface of the hose. In this model, the pipe cavity is of course the coelom, the sheet lining it is the peritoneum, the double supporting tissue is the *mesentery*, that part of it which is in contact with the hose is the serous coat, and the hose itself is the intestine (Figs. 374 and 375).

Liver and pancreas are produced as out-pocketings of the endodermal lining of the intestine. The pancreas develops from two separate outgrowths which later fuse. Each outgrowth branches repeatedly. The liver bud produces epithelial cords which penetrate like roots into the surrounding tissues and there produce a spongy mass which later differentiates into the liver tissue.

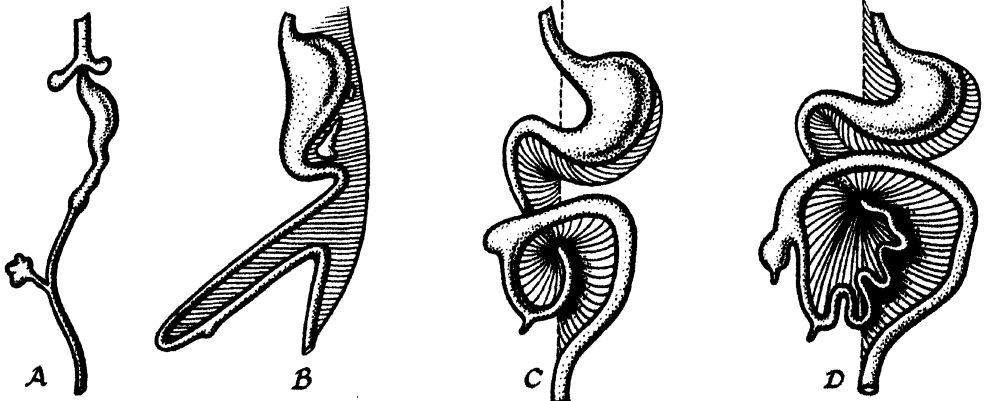
The development and general structure of the vertebrate digestive system differ relatively little from class to class. Differences, though apparently almost limitless in number, are primarily in the particular adaptation of the characteristic structures to special modes of life and special environments.

Adaptive Variations

Of the wide variety of vertebrate mouths, teeth, tongues, and beaks, only a few aspects can be described here.

Teeth. Teeth first appeared in primitive fishes, along with jaws — they were still absent in the cyclostomes. As modifications of calcified skin armor-plates in early jawed fishes,

Fig. 374. Development of the mesenteries and windings of the alimentary canal in the human embryo. In A are shown the spindle-shaped stomach, the lung buds, and the beginning of the liver in the form of a median diverticulum; in B the peritoneum with pancreas and spleen; in C and D the development of the omentum and the lesser peritoneal cavity.



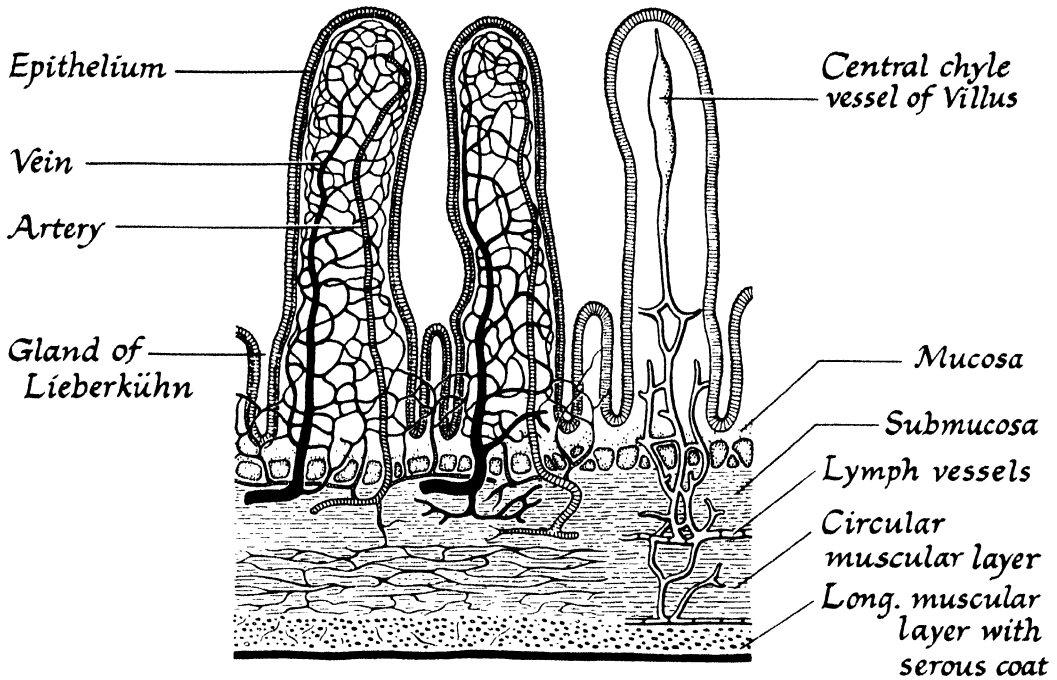


Fig. 375. Schematic transverse section of the human small intestine. (After F. P. Mall.)

teeth appear to have had considerable selective value in those forms where they occurred (Fig. 376). For there, manipulated by the newly evolved jaws, they became effective weapons. For countless millions of years, teeth were simple prongs or daggers used to hold and kill struggling prey. It is significant that with few exceptions, the lower vertebrates are still carnivorous. The primitive tooth is effective as a grasping organ, but wholly ineffective in chewing plant food. Despite other primitive characteristics, some fishes and reptiles evolved grinding teeth and thus became adapted to eating plant food. Generally, however, the complex grinding tooth of the herbivore was not evolved until the period of the mammals, and the primitive teeth of the herbivorous dinosaurs may have been one of the factors that led to their extinction. The acquisition of grinding teeth unlocked for vertebrates the huge new untapped source of energy, the land plants, and was a prime factor in vertebrate multiplication and diversification. The variety of mammalian carnivores, no less than of her-

bivores, was thus made possible, for without the latter, the former would of necessity be few. Today fully 50 per cent of all mammalian species are herbivores, and in numbers they far exceed the carnivores, as they must.

In primitive vertebrates teeth are replaced throughout life. But improved and more permanent teeth brought limited powers of replacement, and now mammals have only two sets, probably reduced from an original four. Mammalian teeth differ from those of all other vertebrates by being set in cavities, or alveoli, in the jawbone, and are widely varied in form and structure for special purposes, even within a single individual. Most mammals have incisors for cutting, canines for tearing and killing, and molars for grinding. One form or the other is frequently emphasized, depending upon the mode of nutrition. Thus in addition to grinding molars, the rodents have highly specialized cutting teeth which grow throughout life and have chisel edges on uppers and lowers which are kept sharp by rubbing against each other. Ruminants, like cows, as well as some

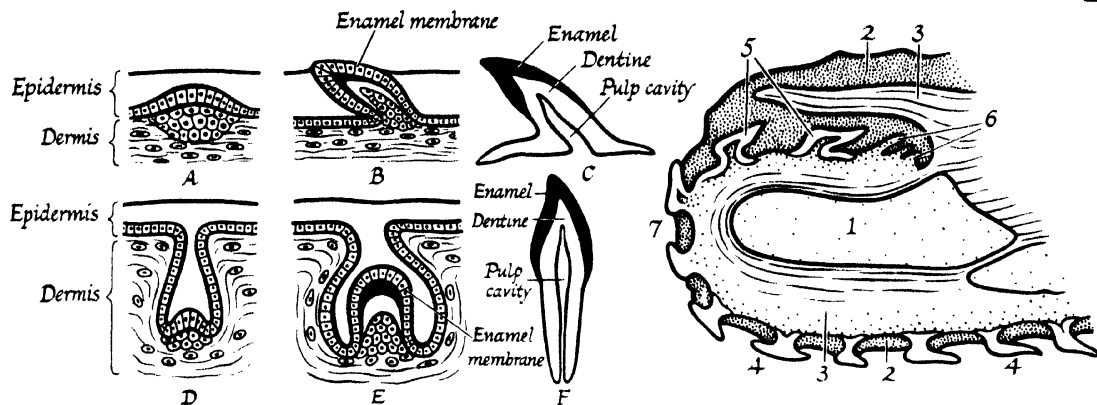


Fig. 376. Development of shark scales and vertebrate teeth. Left: A, B, C, formation of a shark scale. D, E, F, formation of a tooth. Right: 1, cartilage of lower jaw; 2, epidermis; 3, dermis; 4, placoid scale; 5, embryonic teeth; 6, tooth papillae for replacement teeth; 7, anterior rim of lower jaw.

less highly specialized herbivores, have molars with folds of alternate hard and soft material, so that as they wear down, the hard parts produce ridges that stand above the softer material, thus assuring a perpetually rough surface. Carnivores have shear-like molars that shred and cut.

Similarity of tooth structure does not always indicate close relationship. Unrelated species have often evolved remarkably similar tooth-forms as a result of similar habits and needs. Thus the bear-like Australian wombat (*Phascodomys*) has teeth remarkably like those of the common rodents of the rest of the world. The Tasmanian wolf (*Thylacinus*), a marsupial, has the teeth of a carnivore. These similar tooth structures are examples of convergent evolution.

Some vertebrates, like some fishes, amphibians, and reptiles, and of course the birds, have evolved horny beaks and have lost their teeth. Characteristic of this condition are the birds and turtles. Of particular interest are the birds, in which the function of the teeth, possessed by their ancestors, has been taken over by the grinding gizzard.

Tongues. In fishes the tongue is rudimentary. In amphibians and reptiles it reaches a higher development, serving as a snare and tactile organ; while in birds and mammals it undergoes kaleidoscopic variations. In the tongues of mammals muscular development surpasses that in any other vertebrates, and the organ

assists in chewing by manipulating food between the grinding surfaces of the teeth. In some specialized mammals which have lost their teeth, the tongue has completely taken over the function of securing and holding food. This adaptation appears in the scaly anteater (*Manis*) and in the great anteater (*Myrmecophaga*), where the tongue is a sticky agile organ, almost a tentacle, that hauls ants and termites into the mouth. Again, despite great similarity of mouth structure and food habits, these two animals are not closely related. The tongue may be modified as a prehensile organ (cattle), as a grooming instrument and bone scraper (cats), as a heat-radiating organ and drinking ladle, as well as a grooming instrument (dogs), as a sticky trap (frogs, chameleons, woodpeckers), or as an organ of touch (snakes). In mammals the chemical sense of taste is almost wholly confined to the tongue, and the tongue of a cow, for example, may contain as many as 32,000 taste buds.

Glandular equipment is usually absent in the mouths of aquatic vertebrates, even in higher ones such as turtles and whales, and where the mouth is equipped with glands, these are usually limited to the secretion of mucin. Many mammals, however, have salivary glands, which secrete hydrolyzing enzymes in addition to mucin. In some highly specialized vertebrates, such as some snakes, the oral glands secrete albuminous fluids that are highly toxic (venom), and may be injected into

a victim through hollow teeth. In all cases, the secretion of the glands is closely adapted to the type of food eaten.

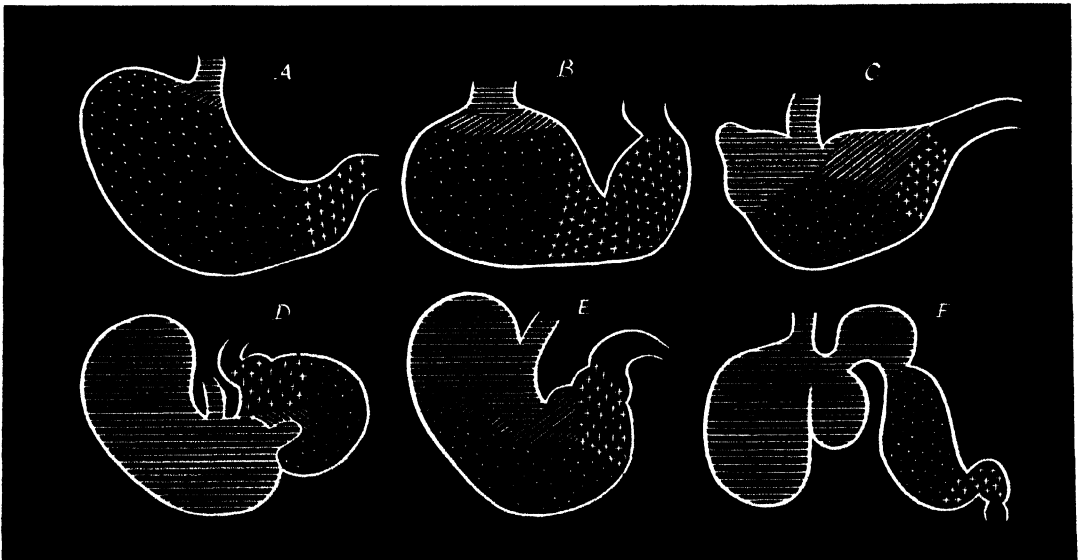
The Esophagus. Although varying considerably from organism to organism, the esophagus is limited as to variety. It is characteristically large and highly distensible in lower vertebrates, where large unprepared masses of food are swallowed whole. Only in mammals is it usually narrow, and able to accommodate only small well-prepared portions of food. In birds, a peculiar distention of the esophagus, the crop, serves for the storing and preliminary softening of food. Crop glands, in some birds, such as pigeons, produce a milky secretion that is fed to the young, and, like milk secretion in mammals, is under the control of prolactin.

The Stomach. This organ shows considerable variation in form and function, though less than teeth and tongue. It serves as a sac for the temporary storage of rapidly ingested food, for mechanical maceration, and for chemical digestion. In the duckbilled platypus, as in the spiny anteater (*Echidna*), the stomach is non-glandular; in the horse it is partly glandular and partly non-glandular, while in most carnivores and in man it is almost entirely glandular (Fig. 377). Ruminants have a remarkably

specialized stomach which is divided into four different compartments. Here large quantities of food can be stored quickly in a large compartment, later to be transferred to another from which it can be regurgitated. In these compartments, bacterial action helps unlock the cellulose for further digestion. Thus the animal can chew its food later, in an isolated spot of its own choosing, and so reduce the hazards of food getting. Upon being reswallowed, the food is directed by a valve to the third and then the fourth compartment, the last of which is glandular, and here digestion proper occurs.

In some reptiles, and particularly in birds, which have no teeth, maceration is radically different but just as effective. In birds the stomach is divided into two compartments, a thin glandular sac and a heavy muscular sac, the gizzard. Depending on its size, the bird swallows gravel or small stones, and the food, previously softened in the glandular sac, is chewed by the powerful muscles of the gizzard and crushed between the stone fragments it contains. The power of this mechanism is illustrated by the fact that an iron pipe capable of withstanding a crushing force of 437 pounds has been flattened in the gizzard of a turkey.

Fig. 377. Vertebrate stomachs. A, Man; B, Dog; C, Rat; D, Hamster; E, Horse; F, Ruminant. The stratified epithelium of the esophageal region of the stomach is shaded by horizontal lines; the simple epithelium of the stomach shows various glandular regions: slanted lines, cardiac glands; stippled, fundus glands; crosses, pyloric glands. (ABF after Opel, C E after Edelman, D after Toepfler.)



As the stones become rounded and dulled they are replaced by new ones picked up from the ground — a simple operation in contrast to the complex operation of replacing a human tooth.

The Intestine. The intestine and its appendages show little variation beyond what increased efficiency implies. In keeping with their phylogenetic position, cyclostomes show a very simple and primitive device for increasing inner surface, somewhat like that found in the folded intestine of the earthworm, a large fold parallel to the main axis of the intestine. In some sharks, such a fold is spiral, and thus becomes still longer without necessitating a greater total intestinal length. In some fishes, the presence of numerous smaller folds achieves the same end. In some reptiles, and in all birds and mammals, the intestinal lining forms thousands of minute finger-like projections, the villi. A basket-like network of blood vessels projecting into each villus increases the absorbing surface many fold.

Finally, the large intestine. At the point where the small intestine enters the large, frequently guarded by a valve, the large intestine often produces a blind sac, the caecum, which may be large, or quite small or even vestigial. There is no caecum in amphibians, but some reptiles and most birds and mammals have evolved one. It is well developed in most herbivorous forms but much reduced in the carnivores. Rodents and ungulates, or hoofed animals, have well-developed caeca. In horses, the caecum has over twice the capacity of the stomach itself. In man, as in other primates, it is small, and its end is reduced to the notorious vermiform appendix. The structure of

the caecum and its large size in herbivores contrasted with carnivores indicate that it harbors more cellulose-digesting bacteria and so, in herbivores, aids in the utilization of woody foods. The large intestine itself lacks enzyme-secreting glands but may be well supplied with those that secrete mucin. It has no villi, but it serves for further absorption, especially for the reabsorption of water, and for temporary storage of fecal matter.

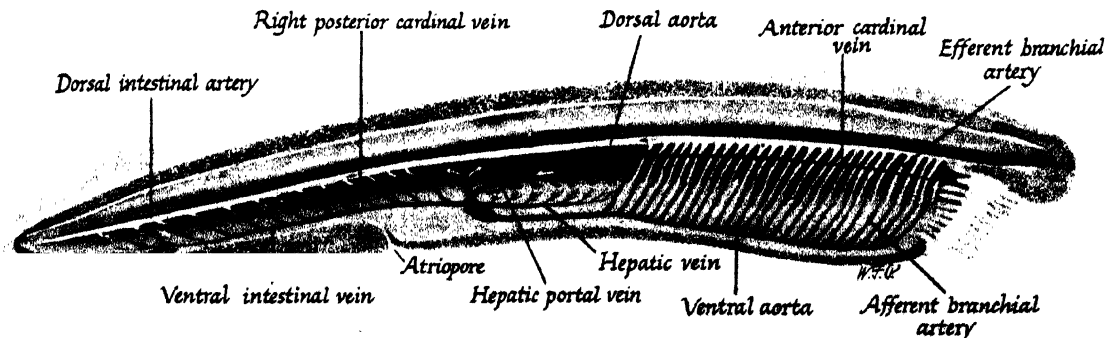
All these are but a few of the many variations to be found in the digestive system. Yet no fundamental deviation from the basic pattern of the vertebrate digestive system appears to have evolved. The plan is so flexible as to be adaptable to almost any environment or food.

THE CIRCULATORY SYSTEM

While simple diffusion transports foods, gases, and soluble wastes in small organisms, even in one as large as *Hydra*, further size was made possible largely through the appearance of a circulatory system, sometimes merely a muscular pump in the body cavity, or a pump which forced the blood through tubes and vessels. In the vertebrates the system has become quite complex, though it appears in its simplest form in the pre-vertebrate *Amphioxus* (Fig. 378).

In all vertebrates the ventral aorta, which in *Amphioxus* still serves as the pumping mechanism, is replaced by a chambered muscular heart, which has evolved from it. The heart is located ventrally, and the blood passes dorsally from it through lateral branchial or aortic arches, whence it continues in a posterior direc-

Fig. 378. Circulatory system of *Amphioxus*. Note the basic similarity to that of the shark (Fig. 379).



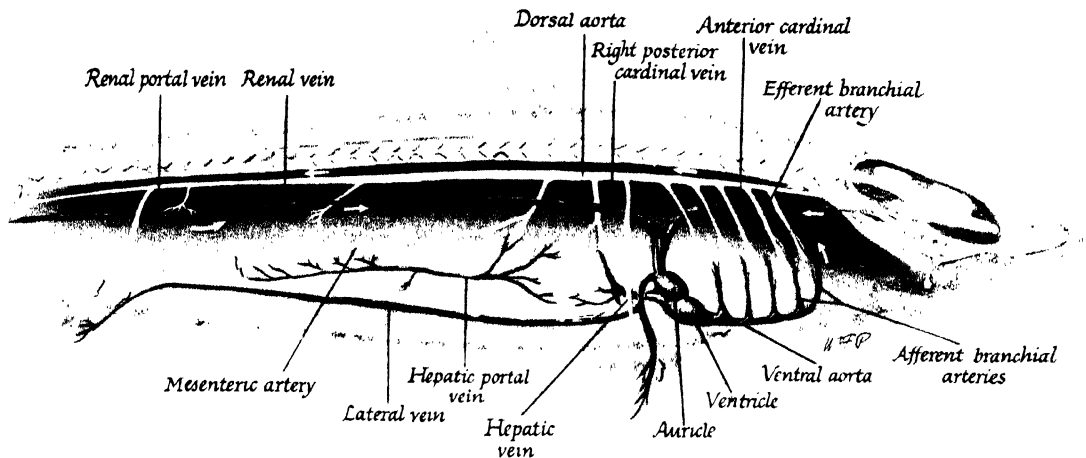


Fig. 379. Circulatory system of the shark.

tion. The arches fuse to form a dorsal aorta, from which numerous smaller branches supply the head and trunk, the muscles and internal organs. From all of these the blood flows back to the ventral vessel via the liver. This is the basic scheme of circulation in all vertebrates, though there are many variations. In higher vertebrates, the chief modifications are associated with the development of lungs, which replace the original gills as breathing organs.

The Heart and Blood

The driving mechanism of circulation, the heart, is a hollow muscle with two, three, or four chambers, depending on the habitus and evolutionary status of the vertebrate organism. One or more thin-walled chambers, the *auricles*, receive returning blood from the veins, while the other chamber or chambers, the *ventricles*, are heavily muscular and drive the blood into the distributing vessels or arteries. Valves in the heart and veins prevent back-flow. The elastic muscular arteries form the distributing system. At their extremities these dwindle to minute permeable vessels, the capillaries, which consist of but a single layer of endothelial cells. Capillaries again merge into increasingly large vessels to form the return-flow system. Veins are thinner-walled, less muscular, and less elastic than arteries, and have valves; otherwise they are much like the arteries in struc-

ture. Veins usually lead into increasingly larger veins or into the heart, but some lead into capillaries again in such special organs as the liver or kidney. Here the capillaries once more reunite to form veins which finally conduct the blood back toward the heart. Smooth muscle cells coat all blood vessels, and under the controlling influence of the autonomic nervous system, such muscle layers, by contracting or relaxing and allowing the vessels to dilate, determine the quantity of blood directed to specific tissues.

The circulating medium, the blood, is a complex fluid with a liquid base, the *plasma*, in which are suspended red and white blood cells. The plasma is an aqueous solution of salts, nutrients, metabolic wastes, hormones, and specific antibodies against toxic substances and invading organisms. Also in solution are gases, such as oxygen, carbon dioxide, and nitrogen. Specific blood proteins help in controlling the rate of osmosis and in the important function of clotting. The red cells carry oxygen in chemical combination with hemoglobin. These cells are typical cells with nuclei, except in mammals, whose red cells, when released into the circulation, have discarded their nuclei. White amoeboid cells, including forms called *lymphocytes*, ingest bacterial organisms, cell debris, and foreign proteins. Thus it is not surprising that a sample of blood, under the

scrutiny of an expert, may tell an eloquent story of the history and present condition of the donor.

Not all of the blood of the circulatory system stays within its vessels. The plasma seeps through the walls of the capillaries and keeps the tissues properly bathed in their necessary liquid medium, now called *lymph*. Were there no device for again removing this, the tissues would soon become swollen and engorged with lymph, as they do in the disease filariasis or elephantiasis, where parasitic filaria clog the lymphatic system. This accessory lymphatic system serves to reabsorb the plasma filtered out of the circulatory system. Throughout the body, the lymph vessels form a branching system of colorless vessels which arise in the intercellular spaces, and like a river system, merge to form, ultimately, two large vessels. One of these, the thoracic duct, drains its lymph, absorbed from the digestive tract and from most of the left as well as from some of the right half of the body, into a large vein coming from the left arm (left subclavian). The other, the right lymphatic duct, drains only the right half of the body and head, and empties into the corresponding right vein. There is no pump to propel the lymph along these vessels, and its flow is consequently slow. Movement and muscular contractions throughout the body cause pressure on the ducts, and since these contain flap-like valves throughout their length, permitting flow only downstream towards the veins, they constantly drain.

Development and Evolution

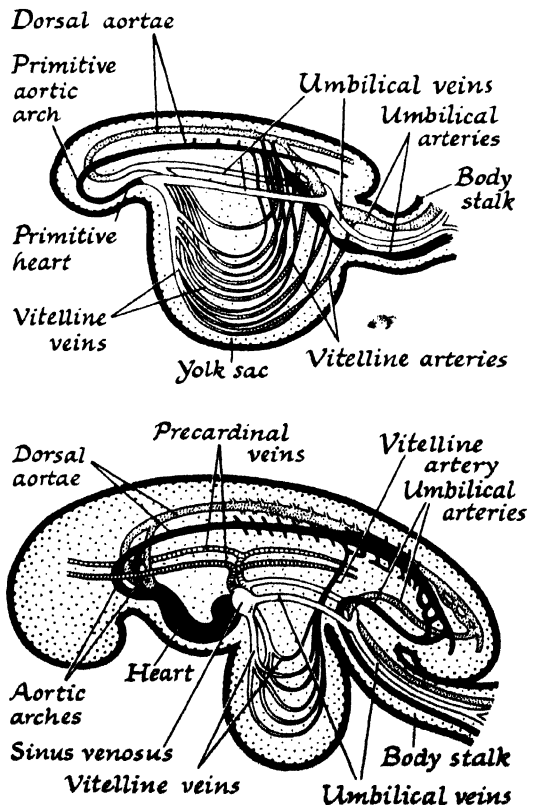
The circulatory systems of mature vertebrates show both outstanding similarities and pronounced differences. These apparent contradictions fit neatly into the scheme of evolutionary theory. In order to understand any one pattern, it is necessary to study the structure and embryonic development of several representative types.

In all vertebrates from the lowest to the highest, blood cells and blood vessels arise from the mesenchyme. In the embryo, islands and cords of mesenchymal cells are formed, which

soon become hollow. The peripheral cells of these cords become flattened and form the endothelial lining of the new blood vessels. Cells locked within the tubes thus formed differentiate into blood cells, and float within a clear fluid, the plasma, which is secreted by the cells of the cord. The original vascular spaces grow and coalesce to form the vascular network of the early embryo. Mesenchyme cells add further coats of muscle and fibrous tissue to the blood vessels and by further fusion and differentiation, determined by the demands of the growing organism, arteries and veins, at first indistinguishable from each other, arise.

The vertebrate heart is at first a tubular structure, but it may develop in different ways, depending on differences in yolk supply and resulting modifications of cleavage. In man, two ventral tubes fuse to form a single primitive heart tube (Fig. 380). The paired dorsal

Fig. 380. Formation of the heart tube and the dorsal aorta in man. Above, at the beginning of somite formation. Below, at twenty somites. (Prentiss, after Felix.)



vessels also fuse, beginning at their posterior ends and continuing forward to the level of the solar plexus, to produce a single descending aorta. Five additional pairs of aortic arches are added to the first pair, and thus the basis of the higher vertebrate circulatory system is established.

The hearts of fishes remain simple and two-chambered, with an auricle and a ventricle, but in higher lunged vertebrates, additional heart chambers form by the growth of partitions in the original tube (Fig. 381). The fact that widely varied adult forms arise from strikingly similar embryonic ones is indeed significant. Probably nowhere is recapitulation more striking than in the formation of the aortic arches. In sharks, six pairs of aortic arches appear and five of them actually function to supply the gills. In higher vertebrates, these same arches methodically develop as though in preparation for their original function. Then peculiar retrogressions produce the strikingly different, asymmetrical plan of a bird or mammal (Fig. 382). The developing aortic arches of a human embryo show this process clearly.

The modifications of the aortic arches are closely related to the evolution of lungs, to the increasing size and importance of appendages, and to generally increasing activity and higher metabolic rate. As gills were losing their function and consequently their selective value, the aortic arches that served them were becoming utilized in other ways, as rudiments for the growth of endocrine glands, for example. And a minor branch of the sixth arch, which first served a network of blood vessels in a pharyngeal pouch (the primitive lung), soon assumed major importance. Increasing activity meant an increased oxygen requirement, and favored the selection of individuals with hearts and vessels that tended to place the pulmonary or lung circuit on an even footing with the systemic or body circuit. The typical plan of a fish is based upon a two-chambered heart, the auricle that receives the blood from the body, and the heavily muscled ventricle that pumps it out through the aorta and the paired aortic

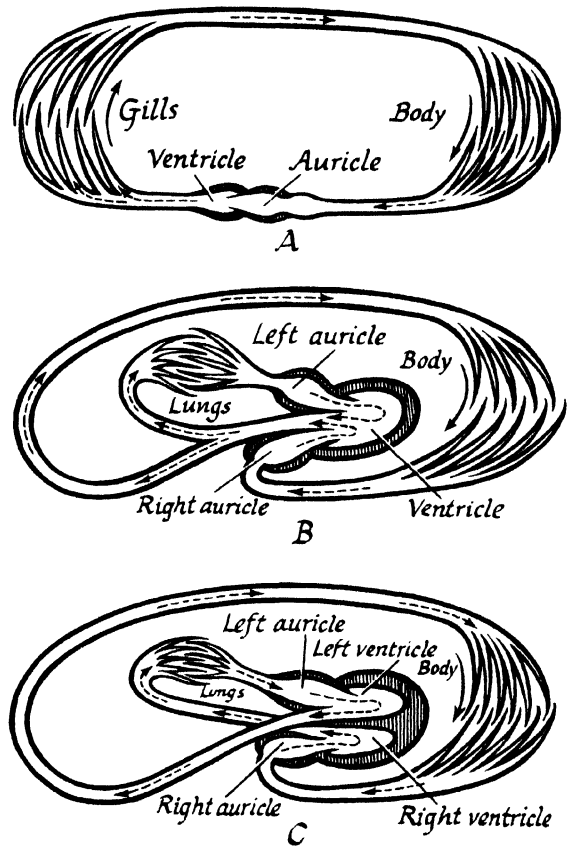


Fig. 381. Three variants of vertebrate circulation. A, fish; B, amphibian; C, mammal. Note auricles, ventricles, gills, lungs, body capillaries. In C all of the blood has to be passed through the aerating system before it is again released to the body.

arches to the capillary network of the gills, whence it is distributed to capillary systems in all parts of the body. But with the appearance of the lung in lungfishes and amphibians, the gills became gradually functionless and their capillary system useless, though a branch of the sixth aortic arch became the pulmonary artery. When oxygenated blood returns from the lungs to the heart in such animals, it is received by a separate auricle, which pumps it into the single ventricle. Here it is partially mingled with non-oxygenated blood returning from the body and delivered through the other auricle. By means of valves and incomplete partitions, however, a complete mingling in the ventricle is avoided, and the blood is so injected into the aorta that most of the unox-

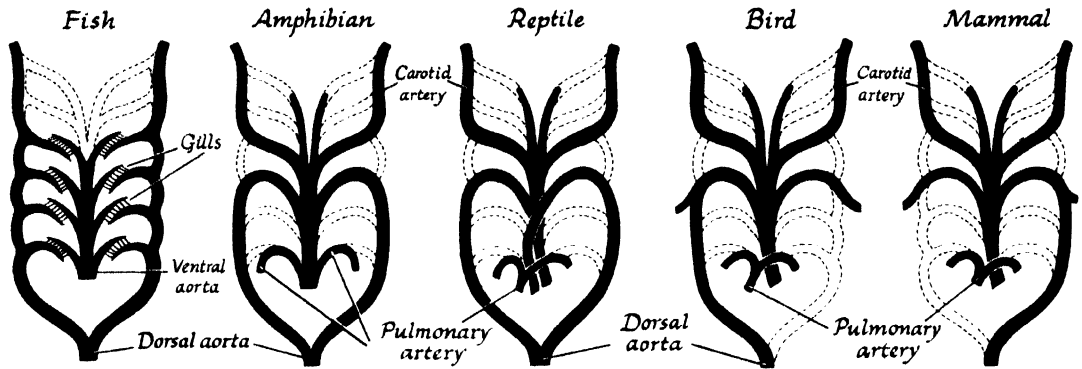


Fig. 382. Transformation of the six pairs of primitive gill arteries in vertebrates. Dash-lines indicate parts of the arches that have disappeared.

generated blood passes into the pulmonary arteries to the lung, the mixed blood passes into the systemic circuit, and most of the relatively well oxygenated blood is shunted to a vessel that leads to the head.

This system has certain advantages over that of the fishes, for in the latter, the heart must furnish sufficient pressure to push the blood through two successive capillary systems, first those of the gills and then those of the entire body. Theoretically, the system could be much improved by inserting a supplementary pump between these two capillary systems, thus reducing the pressure in the gill capillaries and making it possible for them to be more delicate and more permeable. In principle, the amphibians have indeed taken a step in that direction, and the birds and mammals have perfected the scheme, producing a closed double circuit (Fig. 381). Where the fishes have one loop from the heart and back to it again, and the amphibians have two parallel loops, birds and mammals have two completely separate loops in series. Thus the advantage of aerating all the blood each time it goes around, as in the fish, is combined with the advantage of a pump before each major capillary system. The equivalent of a second two-chambered heart has been inserted in the systemic circuit.

THE RESPIRATORY SYSTEM

Oxidation of organic compounds, especially glucose, is the basis of most animal metabolism.

Since oxygen is carried to the individual cells throughout the body by the specialized red cells which form a considerable part of the blood, the circulatory system functions as an integral part of the respiratory system. It is similarly an essential adjunct to all other organ systems. In practice, the respiratory system is considered to be that organ system which makes possible the proper ventilation of the blood, enabling it to absorb oxygen and dispose of carbon dioxide. It includes gills or lungs and the apparatus that circulates water or air over these structures.

Evolution, Structure, and Function

As organisms increase in size, and as their integument correspondingly increases in thickness, gas exchange through the outer surface becomes inadequate. Invertebrates have evolved increased respiratory surfaces by leaf-like or feather-like outfoldings of the ectoderm or endoderm, in various parts of the body. In chordates, increase of the respiratory surface was first achieved through utilization of the digestive tract, as in *Amphioxus*. Here increased vascularization of the perforated wall of the pharynx offered sufficient contact between blood and water to supply the needs of the organism. The inefficiency of the absorbing tissues was made good by the extensiveness of the system. *Amphioxus* develops as many as sixty-nine pairs of gill-slits. In the cyclostomes, the slits are enlarged to form seven pockets, or pouches, lined with vascular endodermal tissue

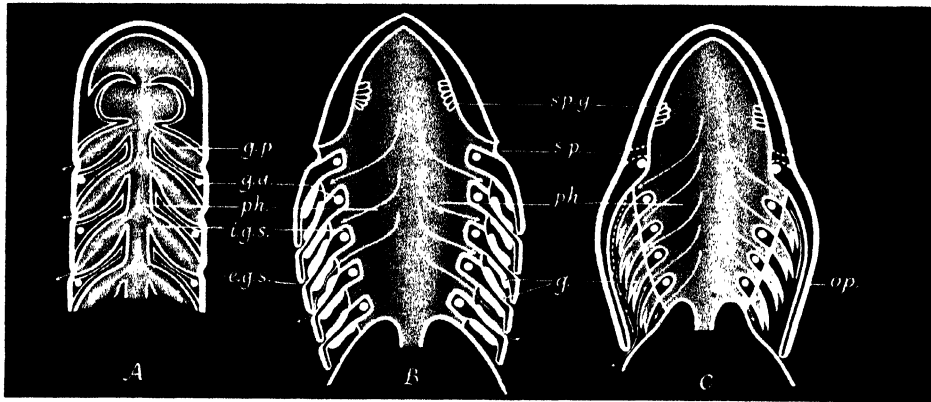


Fig. 383. Dorsal head sections showing gill arches. *A.* Cyclostome, *B.* Shark, *C.* Bony fish. *g.p.*, gill pouch; *g.a.*, gill arch; *ph.*, pharynx; *i.g.s.*, internal gill slits; *e.g.s.*, external gill slits; *sp.g.*, spiracle gill; *sp.*, spiracle; *g.*, gill; *op.*, operculum or covering.

(Fig. 383), and each has an internal and an external opening. In sharks and other cartilaginous fishes the respiratory tissue is ectodermal in origin, and forms numerous leaf-like gills on the exterior or lateral edge of the branchial arches. Only five arches are generally used, though there may be six or even eight. Each cleft still has separate internal and external openings, but each branchial arch grows a skin flap on its outer edge which covers and protects the cleft behind it.

In the bony fishes, the first arch has no gills but supports a skin-fold, the *operculum*, which extends completely over the remaining four gill-bearing arches, thus forming, in effect, a space around them. Internally, each cleft still has its own opening, protected by a comb or screen of bristle- or tooth-like projections which prevent food particles from passing out through the gills.

The gill structure is ideally suited to expose a maximum surface within a limited space (Fig. 384). Each leaf of the fringe that covers the branchial arch is composed of minute leaflets, much as a fern frond is broken into leaflets, thus greatly increasing the surface. The principle is much like that employed in the construction of air-cooled engines, where dozens of fins, as on the outer walls of a motor-cycle engine, increase the surface for more effi-

cient radiation of heat. Within each leaf of a gill, an efficient capillary system distributes the blood for aeration. Gills, then, arise from lateral clefts of the pharynx, so constructed as to permit a circulation of oxygen-bearing water over the vascular lining of the pharynx. Their efficiency rises tremendously by the development of a local vascular network and by increased exposed gill surface. Thus in *Amphioxus* almost half the alimentary tract is devoted to respiration; in the cyclostomes about one-sixth; in cartilaginous fishes from one-seventh to one-ninth, while in bony fishes the entire respiratory structure is confined to a small region entirely within the head.

Far fewer mechanical difficulties are involved in absorbing oxygen from the water than in absorbing it from air. Since living organisms are largely composed of water, exposure of a large permeable surface to the air exposes the tissue to damage not only by mechanical injury but by desiccation. Except for this fact, air-breathing offers great advantages, because air is far richer in oxygen. At normal pressure, and at 0° C., water contains 0.96 per cent oxygen by volume; at 15° this is reduced to 0.68 per cent. But air contains approximately 21 per cent oxygen. Organisms capable of tapping atmospheric oxygen are rewarded by a greatly increased metabolic rate. How real

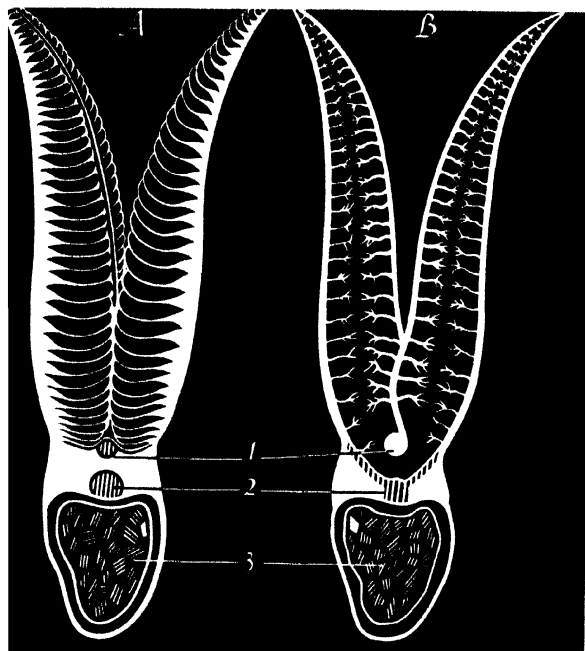


Fig. 384. Cross section through a gill arch with a pair of gills attached. 1. gill artery; 2. gill vein; 3. gill arch; A. surface view; B. internal structure.

this reward is, is expressed by the fact that approximately 80 per cent of all modern metazoan species are land animals. It is also expressed in the contrasted rates of metabolism of water and land animals as measured by the ratio of carbon dioxide production to body-weight.

Water Animals

oyster	.02*
leech	.03
mussel	.05
crayfish	.06
dogfish	.09
shrimp	.18
minnow	.22

Land Animals

lizard	2.81
man	6.48
calf	7.8
rabbit	14.0
chicken	27.0

*CO₂ expressed in mg. per gram of body-weight.
After Jolyet & Regnard.

It is thus not surprising that many different structures which give some access to atmospheric oxygen have been selected for survival and further modification and development. Of these, three main types can be traced among vertebrates, in addition to the makeshift development in some fishes which oxygenate water by bubbling air over it as it passes through their gills. The simplest direct adaptation to air breathing is found in certain fishes, the loaches, which rise to the surface to gulp air through the mouth. The air then passes down the intestinal tract to the posterior region, which is especially well supplied with capillaries, and so actually serves as a lung. Finally the air is exhaled through the anus.

In still another group of fishes, the anabantids, among which is the well-known Siamese fighting fish, *Betta*, there is an air chamber above the gills. A labyrinthine organ within this chamber, covered with a richly vascular epithelium, increases the respiratory surface. With its mouth the fish gulps air into this structure, and its effectiveness is proved by the fact that fish so equipped can live in water which contains no oxygen. Indeed, some have become so dependent on this source of oxygen that they die if prevented from reaching the air at the surface, even though the water in which they are living is normally oxygenated.

Finally — and this was the most successful adaptation of the three — air bladders were evolved in numerous groups of fishes, perhaps quite independently. Such bladders arose from either the dorsal or the ventral side of the pharynx. In many modern fishes, the bladder has lost its connection with the pharynx and serves only as a hydrostatic or buoying organ. It may be limited to this function even where the pharyngeal connection remains. When so used, its position on the dorsal side is functional in preserving equilibrium. Anatomical and embryological evidence suggests that the last gill pouches may have given rise to this primitive air bladder or lung. It was the continued evolution of such a lung that finally opened the land as a habitat to the vertebrates. But lungs alone do not make a land animal, as

is shown by the fact that certain lung fishes actually have more efficient lungs than some amphibians. Indeed, some small amphibians have lost their lungs altogether, and breathe only through their skins and through vascular throat membranes. Other amphibians retain gills in addition to their lungs throughout life. In most cases amphibians first produce functional gills, which correspond morphologically to those of the bony fishes in being pharyngeal and ectodermal in origin, before they metamorphose and develop functional lungs.

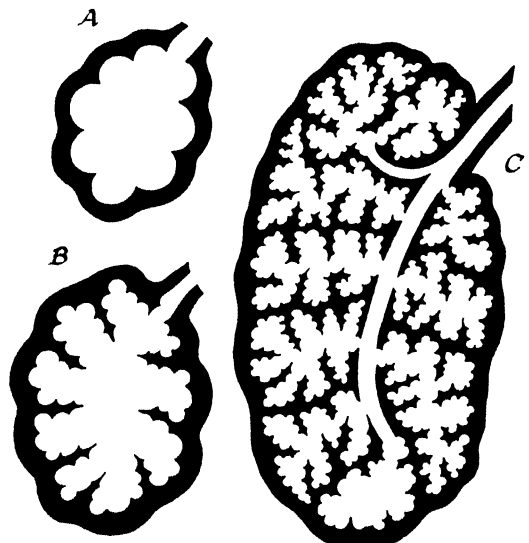
Once the functional lung had appeared, its further evolution was almost inevitable. Since its function is gas exchange, any improvement would have to consist of increased capacity for diffusion. This could occur by simple increase in size or by increase of inner surface, or by improved ventilation. All of these things happened. The increase in inner surface by partitioning may be traced from class to class in land vertebrates. Where the inside of the lung of an amphibian may be no more than a smooth-walled bag, that of a mammal is an intricate mass of clusters of tiny sacs, the *alveoli*, each intimately surrounded with a capillary network (Fig. 385). In general, reptiles have more efficient lungs than amphibians, mammals more efficient ones than reptiles. Birds, especially active fliers, have the best lungs of all.

The ventilating mechanism also differs from class to class. In some groups, as in frogs, the air is pressed from the mouth into the lungs by throat action. In others, as in reptiles, the body cavity is enlarged by pulling the partially folded ribs forward. The air is then "sucked" into the lungs by the reduction of pressure in the body cavity around them. In mammals, a similar principle is employed, but with the addition of a muscular bellows mechanism, the *diaphragm*, which separates the chest cavity from the abdominal cavity. Air may be "drawn" into the elastic lungs either by raising the ribs, lowering the diaphragm by contracting its muscle fibers, or usually, both together. Expiration is achieved by the elasticity of the lungs, which contract and deflate, just as a rubber balloon does, or by forceful contraction

of the abdominal muscles against the viscera and thus against the diaphragm.

In all these systems, the efficiency of the lung mechanism is lessened by the fact that it is intermittent. Moreover, it is mechanically impossible to exhale all air from the lungs. Thus, the fresh air rushing in becomes mixed with the inferior residual air. The system is inefficient for much the same reason as the sac-like digestive system of *Hydra* is inefficient. If the power were granted us to design a nearly ideal system, we would probably make it a continuous one, just as the digestive system of higher organisms has become continuous. We might envision a tubular or labyrinthine finely chambered lung, with an intake opening at one end and an exhaust at the other. A valved bellows could then supply a continuous stream of air. This system may appear unconventional, but actually we should be surprised that something like it has never evolved. Imperfect as is the intestinal lung of the loaches, it is based upon this very scheme, although the fact that it developed from an organ already specialized for another function was not fortunate. The lung of the birds, in its own way, has come close to evolving

Fig. 385. Diagrams illustrating the scheme of lung development whereby increased surface is obtained by partitioning and sub-partitioning. A. Lower amphibian. B. Higher amphibian and reptile. C. Bird and mammal.

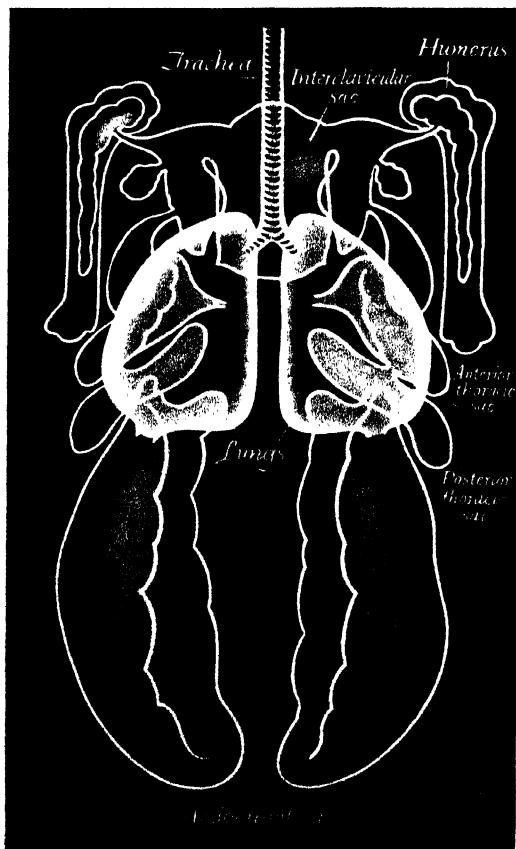


ing a flow-through system, but still appears to be a makeshift. By a series of attached air sacs (Fig. 386), the lung can be ventilated in both directions. The sacs extend posteriorly into the tip of the abdominal cavity, between the ribs, between the vertebrae of the neck, and even into the hollow bones of the wings. As fresh air is drawn into this extensive system, residual air already in the lungs is exhausted into the air sacs, allowing complete ventilation of the lungs with unmixed fresh air. Expiration removes the air within the lungs, as well as some of the air in the sacs. This system appears to work semi-automatically during flight, for the rush of air inflates the lungs and air sacs, and only periodic abdominal contractions are necessary to discharge it.

Development of the Lung

In its embryonic development, the lung clearly originates from the pharyngeal region

Fig. 386. Airsack system of the pigeon. (After Heider).



of the gut (Fig. 387). It arises as a groove in the floor of the pharynx, pushes out as a bud-like structure ventral to the gut, divides and lengthens, and soon displays the basic lung pattern. Branches of the pulmonary vessels grow down and into it with perfect coordination. Growth of the lung continues until the mature individual attains full size.

THE EXCRETORY SYSTEM

In all but minute and very simple animals the excess salts and nitrogenous compounds produced by metabolism are carried by the blood to excretory organs, by which they are eliminated from the body. The simple beginnings of these organs appear in the flame cells of *Planaria*, and they become increasingly efficient in the segmental nephridia of the earthworm, where a small ciliated funnel draws a stream of body fluid containing waste into a coiled tube, and also filters wastes directly from the blood vessels which supply it.

A strikingly similar arrangement is found in the lower vertebrates, and a modified form of the same thing in higher ones. The blood passes first through a filter, where water and all kinds of solutes are removed, only the blood proteins and cells being kept back. Then the same blood is circulated around a long coiled nephric tubule, and here, by processes little understood, virtually all the sugars, amino acids, certain salts, and most of the water are selectively reabsorbed, leaving behind in the tubule for ultimate discharge to the outside the urine — water now heavily freighted with excess and waste substances.

As we trace the evolution and individual development of the structures by which these processes are performed, it will become apparent that another system is always more or less closely associated with the excretory or urinary system, namely the reproductive. The two together are customarily referred to as the *urogenital system*, and neither can be fully understood without studying the other.

Structure and Development

The three stages in the evolution of the vertebrate kidney are all clearly illustrated in the

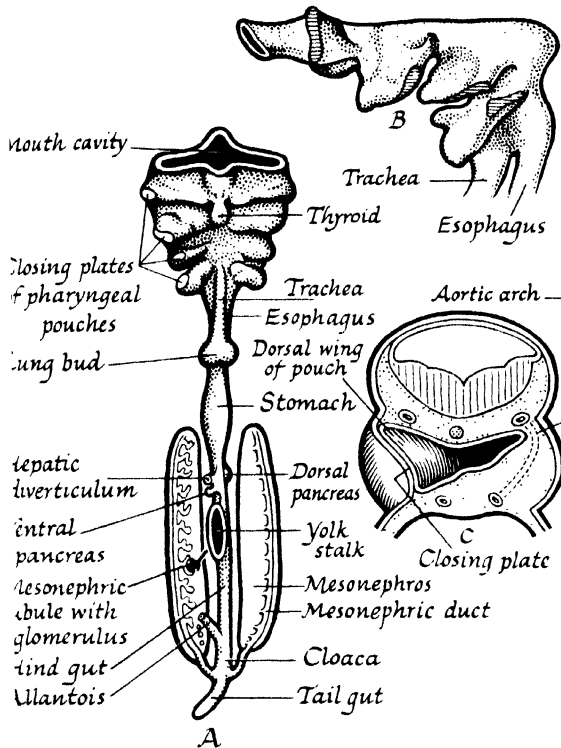


Fig. 387. The early human pharynx. *A.* Endodermal tract at 5 mm. in ventral view. *B.* Pharynx at 7.5 mm. *C.* Pharynx at 8 mm. (Adapted by Prentiss.)

development of the kidney of a human being. Early in the development of the human embryo there appears on each side of the body, between the body somites and the coelomic cavity, a strip of tissue called the *nephrotome* (Fig. 389). From it grow buds, one to each body segment, that develop into tubules, each with one end leading into the coelomic cavity while the other end grows back, parallel to the body axis, until it meets and fuses with the tubule in the next segment. Thus there forms on each side of the body a long, continuous duct with a tubule leading off to the side in each segment, and opening into the coelom. The open tubules are termed *pronephric tubules*, and the common duct the *pronephric duct*. A vascular knob, the *glomerulus*, appears on the wall of the coelom near the ciliated funnel

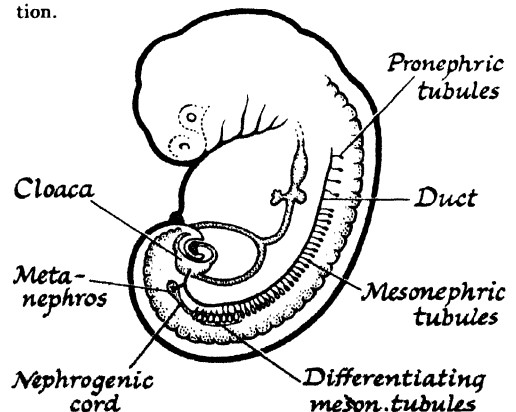
whereby each pronephric tubule opens into the coelom.

About seven pairs of pronephric tubules form in the human embryo, but strangely, the most anterior ones begin to degenerate even before the last ones form. And none of them ever function — they appear to be entirely vestigial structures. In fact, by the time the lower end of the duct reaches its destination in the cloaca, the vestibule of the intestinal opening, all of the pronephric tubules have degenerated and disappeared, and only the duct itself persists.

At about this time, the next posterior portion of the nephrotome (8th segment on) becomes active and produces the *mesonephric tubules*. These are much like those of the pronephros, but instead of forming a new common duct, their medial ends fuse with the growing pronephric (now mesonephric) duct. Oddly, these tubules do not follow the segmental structure, for as many as nine of them may lie within a single somite and about thirty are present at the height of the mesonephric development. Moreover, the free ends of the tubules do not open into the coelom but remain closed. The glomerular knot of capillaries beside each tubule pushes into the cup-like end of the tubule and the whole structure becomes a ball-shaped cup with a double wall, known as a *Bowman's capsule* (Fig. 393).

New tubules continue to form at the posterior end of the series and the forward ones again begin to degenerate. It is difficult to avoid the impression that the organism is repeating a pattern that has lost its original significance — and this is probably just what is

Fig. 388. Locations and relations of the three kidney-types in mammals (semi-diagrammatic). Lateral section.



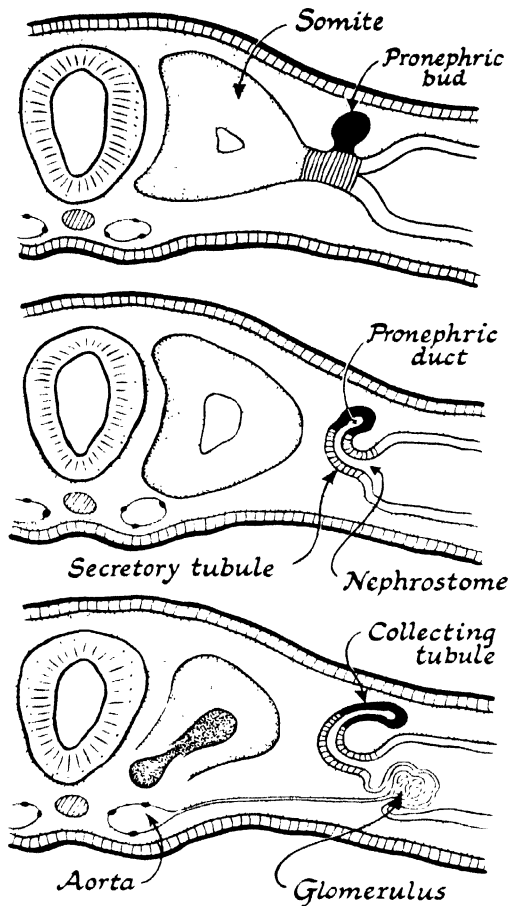


Fig. 389. Development of human pronephric tubule; transverse sections of early embryos (semi-diagrammatic). Note the glomerulus.

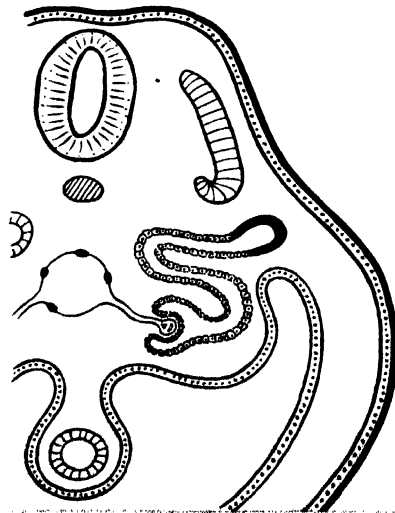
happening. Some of the tubules appear to function briefly as organs of excretion, but all of them soon disappear again, leaving only the continuation of the pronephric duct, here called the *mesonephric* or *Wolffian duct*. Even this is not part of the final excretory system, though it is salvaged for a quite unrelated function, that of conducting the male reproductive cells to the outside of the body.

While all this is taking place, a third set of nephric tubules has begun to form. But where the pronephric ones were segmental, and the mesonephric ones were at least arranged in a series, these *metanephric tubules* show no trace of segmental arrangement, and form a dense

cluster which ultimately becomes the permanent kidney. This new organ, the *metanephros*, is an astonishing example of precision and coordination in the growth and orientation of parts apparently unrelated in origin. At the base of the mesonephric duct there first appears a bud, which grows and produces a branching system of tubes. At the same time, cells of the nephrotome form blind tubules which at one end produce Bowman's capsules, and at the other unerringly establish contact with one of the branching tubes budded from the mesonephric duct (Fig. 388). Blood vessels grow into the Bowman's capsule as it develops, producing the glomerulus and completing the metanephric unit. The metanephric bud thus provides the collecting tubules, while the tissue of the nephrotome produces the Bowman's capsules and the secretory *uriniferous tubules*, together known as a *Malpighian body*.

The system of collecting tubules continues to grow and branch for some time, and the growing nephrogenic tissue continues to originate new secretory tubules at the periphery of the growing organ. Once again the first formed tubules degenerate, until, in the permanent and completed kidney, about 1,000,000 Malpighian bodies occupy the periphery or *cortex* of the organ, while the collecting tubules occupy the central medulla (Fig. 391). All the collecting tubules empty into a funnel-shaped

Fig. 390. Form and relations of a human mesonephric tubule, shown in transverse section at 5 mm. (semi-diagrammatic).



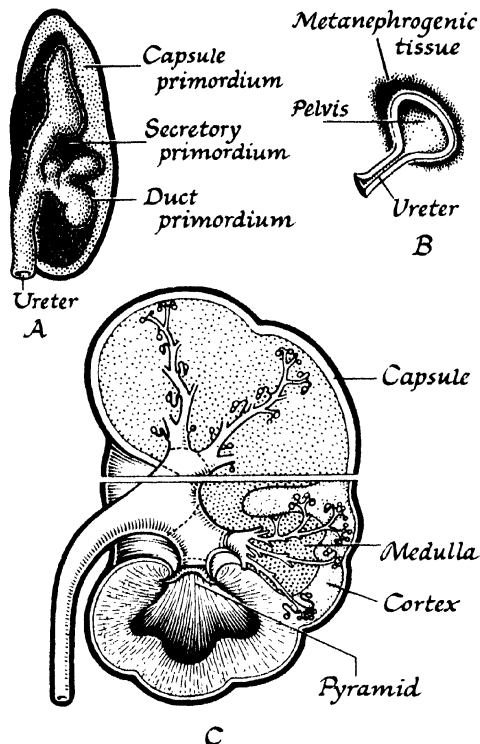


Fig. 391. Organization of the human metanephros. A. Model at 8 mm. B. Model at 12 mm. C. Diagram of relations at nine weeks.

space, the *pelvis*, at the center of the kidney, which continues into the *ureter*, the duct that leads to the *urinary bladder*.

The glomerulus and Bowman's capsule serve as a filter, and the blood pressure supplied by the heart drives some of the blood plasma with most of its soluble freight into the uriniferous tubules. The cells lining these tubules actively work to reabsorb and secrete back into the blood, even against a concentration gradient, those solutes which the body needs, regulating the concentration in the blood of each one to the optimum level, and allowing the unabsorbed fraction, with its wastes, to pass into the collecting tubules, thence down the ureter into the urinary bladder, eventually to be discharged through the *urethra* (Fig. 392).

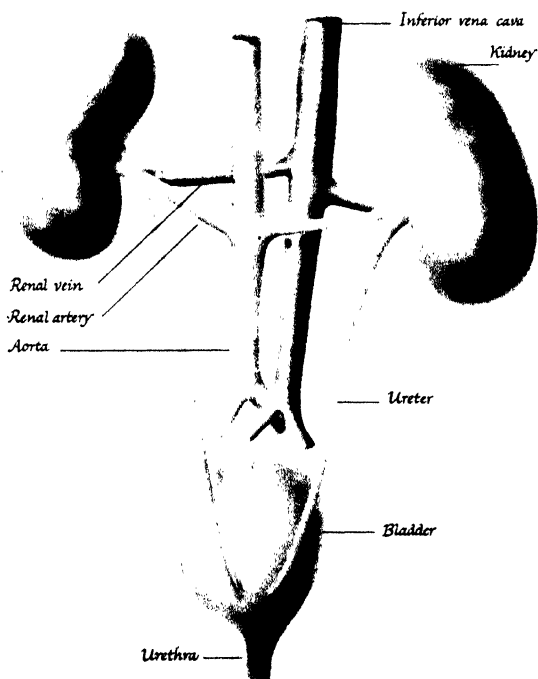
Evolution of the Kidney

The devious development of the mammalian kidney, as illustrated by the human kidney,

like that of many other organs would be wholly incomprehensible but for our knowledge of evolution. A review of the excretory systems of lower and phylogenetically earlier vertebrates displays a sequence of kidney structures fully in accord with the evidence of mammalian embryology. There is no more striking evidence of recapitulation than the development of the kidney.

In the primitive hagfish, a cyclostome, as in the pre-vertebrate *Amphioxus*, a pronephros develops which is never replaced by any other excretory structure. In other vertebrates it is always the first excretory structure to appear, and it is functional in the embryonic or larval life of some fishes and of amphibians generally; in adult forms, however, it is replaced, as in the human embryo, by the mesonephros. In fishes and amphibians the mesonephros is the final excretory structure, and some of its tubules, as well as the entire mesonephric duct, serve the male reproductive processes as well. But in reptiles, birds, and mammals, the mesonephros is but a temporary structure, functional in the earliest part of life or not, but eventually replaced by the metanephros.

Fig. 392. Human urinary system, posterior view.



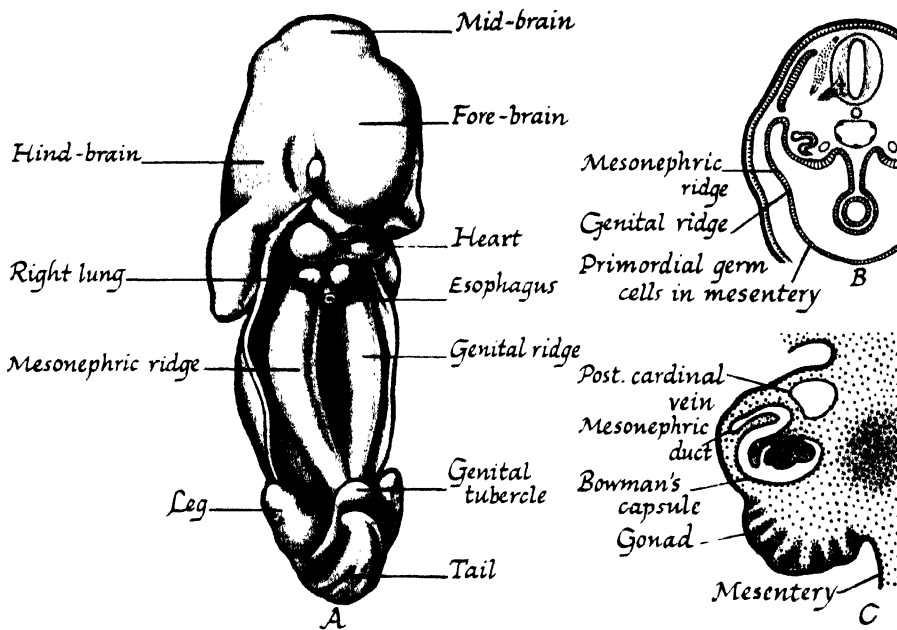


Fig. 393. Urogenital ridge of human embryo. A. Dissection at 9 mm. B. Transverse section at 7 mm. C. Transverse section at 10 mm.

Thus on successive levels of vertebrate evolution, pronephros through mesonephros to metanephros, the Malpighian bodies become increasingly efficient, smaller, and more numerous. With the disappearance of segmental arrangement in the kidney, the walls of the capillaries of the glomeruli become the very walls of the Bowman's capsules, in a more intimate union. The entire excretory function becomes concentrated in a relatively small, compact organ.

THE REPRODUCTIVE SYSTEM

Reproduction in the vertebrates has become vastly more than a simple production and scattering of gametes. The entire reproductive system in the hydra consists only of one or more ovaries and testes. But in a mammalian female it consists of ovaries, oviducts, uterus, vagina, and a complex supporting system of specialized endocrine glands, nerve centers, and devices for the circulation of blood. In the male it consists of testes, collecting tubules, sperm ducts, and a complex organ of copulation, the penis. Nervous, endocrine, and blood-vascular systems are all involved in it. Whereas in the hydra reproduction is a strictly localized phe-

nomenon, in vertebrates the entire organism participates in reproducing and maintaining the species. This is strikingly exhibited in the complete disregard for individual safety displayed by mating males, and the similar individual contempt for danger often shown by females in protecting their young. Perhaps no phase of biology is more complex than that concerned with mating and reproduction.

Besides producing gametes — sperm and egg cells — and depositing them in such a manner that they meet, a successful organism must somehow provide for the growth of the zygote to maturity. The mere mention of these requirements at once suggests scores of ways in which they might be met. In the vertebrates, scores of ways have indeed been evolved.

Origins of the Vertebrate Reproductive System

In the hydra, reproductive cells develop just beneath the ectoderm, and in due time are discharged to the outside. There is no provision for furthering the process of fertilization. In simple vertebrates, conditions are scarcely more advanced. The gonads originate as thickenings of the dorsal epithelium of the coelom (Fig. 393), and under the proper circumstances of

age, season, and so on, the gametes produced in them burst through into the coelom and find their way to the outside through paired pores or ducts. Thus, in the primitive cyclostomes, two genital pores in the mesonephric duct's widened mouth, the urogenital sinus, serve as avenues of escape.

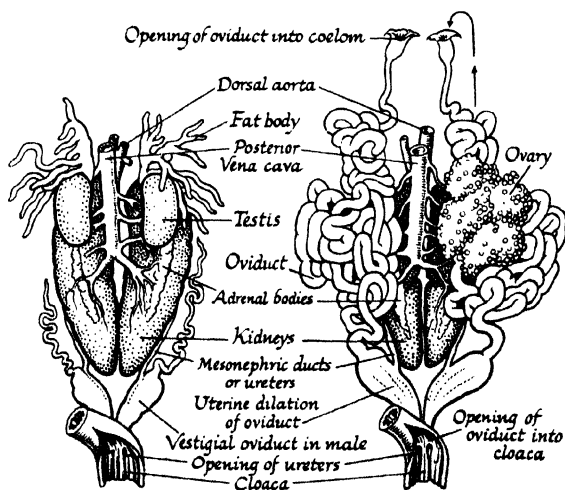
The system does not long remain so simple. Yet nature appears to be frugal. Probably because such adaptation has selective value, two structures seldom appear where one will serve, and often existing structures are salvaged for new uses, as gill arches for jaws and ear-bones. A similar modification took place in the development of the reproductive system. In studying the kidney we have seen that each pronephric tubule consists of a ciliated funnel leading from the coelom to a duct which passes to the outside. It is scarcely surprising, then, that in most vertebrates this already existing pair of channels should come to serve as an exit for gametes. Similarly, as we might expect, not all vertebrates evolved the same system. In many bony fishes, special sperm ducts and oviducts not associated with the excretory system have evolved. But all other vertebrates show a relationship between gonads and kidney ducts which is at first crude but in the higher forms is increasingly differentiated and refined.

In order to trace this evolution properly, it is necessary to recall that as the kidney developed and the first sets of tubules degenerated, the Wolffian (mesonephric) ducts remained. A second parallel pair, the *Müllerian ducts*, also appeared, perhaps by a splitting-off process from the original pairs. Both pairs run lengthwise of the body and empty into the urogenital sinus, a derivative of the cloaca. In successive vertebrate classes, these two sets of ducts, at first parts of the excretory system, become increasingly modified for reproductive functions. In the amphibians, while the mesonephric (Wolffian) duct functions for excretion throughout life, the *Müllerian duct* has become exclusively a part of the reproductive system. In males, some of the most anterior mesonephric tubules become *vasa efferentia* and con-

duct sperm cells from the testis into the mesonephric duct, while the posterior tubules still function in excretion. In females, the mesonephric duct serves only for excretion, while the two partly fused *Müllerian ducts* become specialized *oviducts* and *uterus* (Fig. 394). In males, the *Müllerian duct* is vestigial.

At this stage of vertebrate evolution the pattern is clearly established, and further changes are not fundamental. As the metanephros becomes established in reptiles and all other higher vertebrates, the mesonephros vanishes, and the mesonephric duct becomes an exclusively reproductive structure, the sperm duct or *vas deferens*. Portions of the *Müllerian ducts* develop into specialized reproductive organs, too, as vertebrates produce larger and better eggs or become live-bearing. In reptiles and birds, these ducts evolve elaborate glandular structures for building massive food deposits and for secreting the shell that encases the egg. In mammals, the posterior region of the ducts fuses to make the *uterus*, in which the embryo develops, and contributes to the formation of the *vagina*, which receives the seminal fluid of the male. But the basic plan still remains: the Wolffian duct (the old mesonephric duct) carries the seminal fluid with its suspended sperm; the *Müllerian duct* carries the ova, and in higher vertebrates completes the formation of the egg and houses and nourishes the embryo.

Fig. 394. Urogenital system of frog.



Although a gradual specialization and increase in efficiency can be traced from the lower vertebrates to the higher, differentiation in any one organ system does not necessarily imply similar advances in all others. We consider the production of living young a higher performance than the laying of eggs. This conclusion is, however, only partially justified. The laying of a codfish egg is certainly a simpler process than the bearing of a living infant. But it is a real question whether the specialization necessary to produce a chicken egg is inferior to that necessary to produce a mammalian embryo. Even some fishes still low on the vertebrate scale have highly evolved and perfected reproductive systems. Among the sharks there are more viviparous (live-bearing) than oviparous (egg-laying) species. In large fishes that live in the open ocean, far from shallow bays where eggs could be safely attached, the selective value of bearing living young is apparent. Actually, most sharks, as well as other fishes, are better termed ovoviviparous, for they produce eggs and retain them in the uterus until they hatch. Consequently, the mother contributes little or nothing to the nourishment of the young beyond what is stored in the egg yolk. This is really a simple modification of egg-laying, but it opens the way for various mutations which adapt the retained young so that they can make use of uterine secretions, or even of the tissues of the mother, as a source of supplemental nourishment.

In many sharks this has happened to an astonishing degree. In some the developing offspring eat each other, thus concentrating the stored yolk of numerous individuals into one, which can attain much greater size. Yolk sacs measuring ten inches in diameter have been observed, a product of such cannibalism. In less violently primitive species the uterus and the embryo produce special structures for the exchange of food and wastes. In some rays (*Trygon bleekeri*), relatives of the sharks, the uterus grows glandular teats (trophonemata), which by muscular contractions inject their secretion into the mouth or spiracle of the

embryo. In a certain ray of the Indian Ocean (*Pteroplatea micrura*), two bundles of trophonemata grow through the spiracles of the young and inject milky secretions directly into the alimentary tract of the embryo. In some small sharks (*Mustelus* and others) which live on the ocean bottom, villus-like processes on the vascular yolk-sac of the embryo penetrate the uterine wall, producing a yolk-sac placenta astonishingly like the placental structure of higher mammals. This was known to Aristotle in ancient times, and made him confuse his classification of animals. Thus while in general the care and nourishment of the young gradually improve in the evolutionary scale, exceptions such as these occur in every vertebrate class. It is possible to construct an evolutionary sequence from egg-laying fish to placental mammal, and it is tempting to read some design into the sequence, especially since it is true that a creature such as man could hardly be achieved without a prolonged intrauterine life with placental nourishment. But the primitive shark with a "placental" method of nourishing her young cautions us not to draw conclusions too hastily. Clearly, evolution does not follow a simple straight line.

We may, however, make the following generalization, even though it must be definitely qualified. The more primitive organisms generally survive by sheer weight of numbers, and in general the lowest vertebrates survive by this method. The complex higher vertebrates require a longer period of development. Although this reduces the possible number of offspring, it also reduces the need for greater numbers, since the individual's chances of survival are greatly enhanced. Thus, all along the scale, the reproductive rate is generally in inverse ratio to the degree of complexity and to the survival rate. Yet exceptions are found everywhere, although the birds and mammals, and even the reptiles, never approach the prodigious reproductivity of the amphibians or fishes. Even in the latter groups the trend is not clear cut. A single cod may lay nine million eggs; other fishes may produce only a dozen or fewer living young at a time. Some fishes show

the greatest concern for their eggs and their young; many reptiles, on the other hand, show none at all. Small mammals, not well equipped to protect their young, produce large litters, while larger animals — especially where the young are precocious — produce few, as illustrated by guinea pig and elephant, respectively.

External Structures

The evolution of the external genital structures also illustrates the necessities determined by life on land. Where eggs and sperms are merely discharged into the water, no special structures beyond genital pores are required. But land vertebrates and those which live in the open seas could not survive by any such hit-or-miss method. Except in those land vertebrates, such as amphibians, that return to shallow water for reproduction, the sperm must be conveyed to the egg. This is most simply done by intromission of the seminal fluid directly into the reproductive tract of the female. Organs which make this possible may at first glance seem to be a specific adaptation to land life, but this is not true. In the fishes and in many invertebrates, modifications of previously existing organs perform this function. In sharks the pelvic fins of the male are converted into grooved organs, the *claspers*, which conduct the seminal fluid into the cloaca of the female. In some amphibians (newts), the cloaca of the female is protrusible and acts as an intromittent organ in picking up sperm packets.

In the reptiles and higher vertebrates there is a special copulatory organ, the penis. This structure, at first a grooved erectile organ, as in the turtle and the crocodile, became the characteristic mammalian penis, in which the reptilian groove is completely closed to form a tube, the continuation of the urethra. By a parallel evolution, the terminus of the female tract became transformed into a pouch, the vagina, into which the penis is inserted and the seminal fluid deposited. A high degree of nervous development and coordination accompanied these anatomical changes. In some fishes there is not the slightest visible differ-

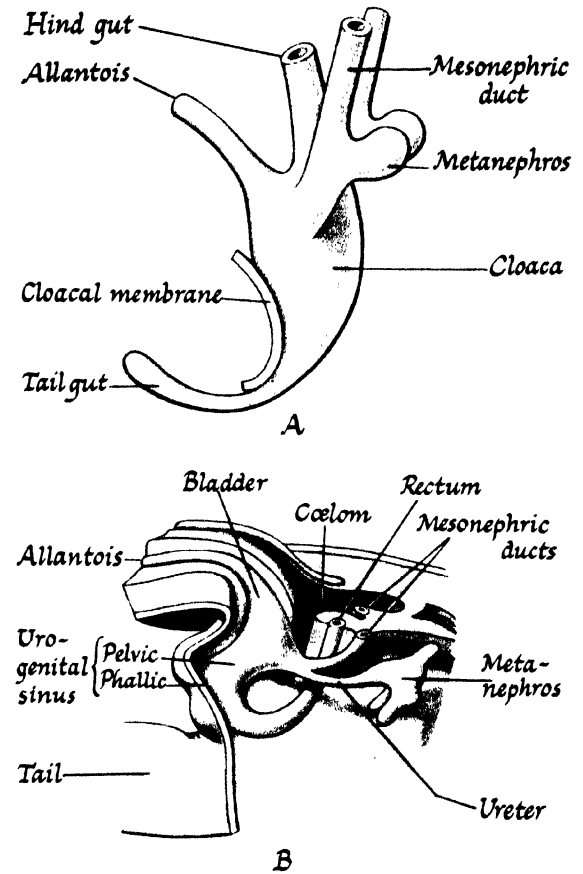


Fig. 395. Development of the human metanephros and cloaca. A, at 4 mm. (after Pohlman); B, at 11 mm. (after Keibel).

ence between the two sexes, yet the male unerringly picks the female out of a group of individuals, where even the highly trained ichthyologist is quite unable to distinguish between them.

There is a wide variation in copulatory structures, particularly in those of the male, though it is not possible to say that one type is better than another, for they all fulfil their function of introducing sperm cells into the reproductive tract of the female. Internal insemination practically guarantees fertilization of any eggs that are present. In man, over a quarter of a billion sperm cells are deposited at one time, and the possibility that all of them will fail to fertilize any mature egg cell present in the oviducts is negligible. There is evidence that a certain volume of sperm is necessary for ferti-

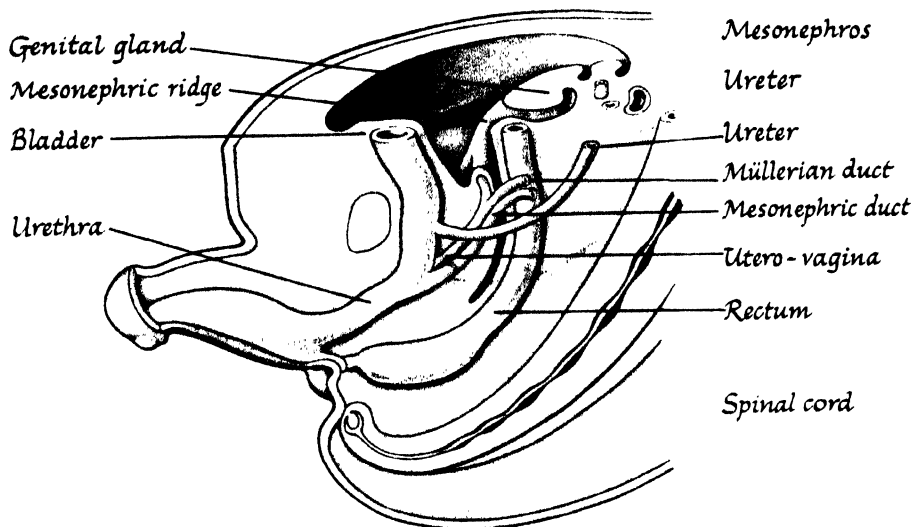


Fig. 396. Later changes in the embryonic human urogenital system; at nine weeks (after Keibel).

lization, even though only one spermatozoon is required.

Embryological Development

The origin of the sperm ducts in the male, and of the oviduct, uterus, and vagina in the female, mentioned earlier, is shown in Figs. 395 and 396. In the human embryo, as in that of lower vertebrates, the development of the external genital organs begins with the formation of the *cloaca*. Here the intestinal and urogenital tracts end in a common chamber, for a while still closed to the outside by a membrane. Soon a septum begins to separate the intestinal from the urogenital portion of the cloaca. The part now reserved for urogenital purposes enlarges and becomes the *urogenital sinus*, similar to that found in the cyclostomes (Fig. 395). Complete division of the cloaca results in an anal opening for the intestine and a separate one for the urogenital tract. The urogenital sinus becomes the *urinary bladder* and the phallic region which bulges out more and more to form a projection, the *genital tubercle* (Fig. 393). It is this which evolves into the penis of the male or the homologous clitoris of the female, which serves only for sexual stimulation. Externally, male and female structures are indistinguishable in the early stages. Internally and externally, the organism at an early age is mor-

phologically neither male nor female, even though its sex was genetically determined at fertilization. As development proceeds, shifts in emphasis mold the originally similar design into the male and female patterns, and we can observe certain homologies. The scrotal swellings of the male, later to form the *scrotal sac* which accommodates the descending testes, are paralleled by the labial swellings in the female, which later become the external labia. Still later in development, the Müllerian duct breaks through into the vestibule, ventral to the urethral opening, and establishes the basic difference in the genitals of male and female. Subsequently, it develops into vagina and uterus.

Abnormalities in adults of both sexes can sometimes be traced to imperfections in embryological development. Thus an imperfect fusion of the right and left Müllerian ducts may cause a duplicate uterus and vagina, a condition which is normal in primitive mammals, but distinctly abnormal in the human being. In males, likewise, the urethral fold may fail to close, and the penis may consequently retain its embryonic similarity to the grooved reptilian organ. Finally, the testes of the male, which develop in the abdominal cavity and later in most mammals slip through a hole in the abdominal wall and enter the scrotal sac, in some instances fail to do so. In higher mammals,

when the testes remain in the abdominal cavity, as they always do in lower vertebrates, it usually results in sterility.

Advances in the vertebrate reproductive system have been mainly in the accessory structures for fertilization and for the housing, protecting, and nourishing of the dependent offspring. The gonads have changed little.

DEVELOPMENTAL MECHANICS

The vertebrate, like every other metazoan, begins its life as a single undifferentiated cell, the fertilized egg or zygote. It is possible to observe directly the changes that occur during its development, but the causes of these changes are not readily apparent. Yet, while science cannot give a full and satisfactory account of the entire phenomenon, it can at least partly break down the development of an animal into sequences of cause and effect, and can partially explain why certain phases of development occur where and when they do, why structures appear long before they have any function, and particularly, whether there is a causal relation between an earlier stage and a later one. The branch of biology devoted to such investigations is known as developmental mechanics or experimental embryology and was pioneered by the German biologist Wilhelm Roux, who published fundamental papers between 1883 and 1900. The problems of development are attacked by altering the conditions under which the whole embryo or its parts develop.

The first stages in the development of the vertebrate are similar to those in *Amphioxus* (pages 381-382). The process may be considerably modified, depending largely on the quantity of stored inert yolk in the egg, but the

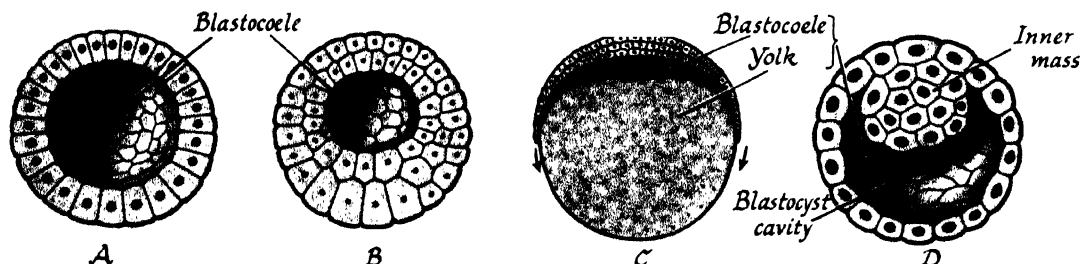
basic plan remains much the same (Fig. 397). By a series of cleavages, the zygote divides into two cells, then into four, eight, and so on, until the cells have arranged themselves in the pattern of a hollow sphere, the blastula. Then invagination of the cells of the vegetal pole results in a double walled cup, the gastrula, or some modification of it. This is followed by stretchings, foldings, and various pinching-off processes until the basic plan of the organism begins to take shape.

The original egg cell is approximately spherical, and at first glance appears to be a uniform cytoplasmic mass containing a nucleus. Yet this structure develops into an elongated bilaterally symmetrical animal, with sharply differentiated head and tail ends. The question arises, what factors, external or internal, establish the planes of symmetry in relation to the spherical egg, for it is inconceivable that an axis would arise without cause.

Closer examination shows that the cytoplasm of the egg is not of uniform structure, but is a mixture of many substances. By whirling the egg rapidly in a centrifuge, an effect equivalent to many thousand times that of gravity can be produced, and ingredients of different specific gravity separate into distinct layers, much as cream separates from milk. To a less marked degree, such separation takes place in the normal egg under normal conditions, so that there are regional differences in composition and behavior of the cytoplasm within it.

It is now known that the future antero-posterior axis of the embryo is determined within the unfertilized egg as a result of the chemical and electrical gradient created by the uneven distribution of substances in it. This axis in

Fig. 397. Hemisected blastula types. A. *Amphioxus*; B. amphibian; C. reptile and bird; D. mammal. A and B are fundamentally comparable; C is a modification of B; D is a modification of C, with loss of yolk. Arrows on C indicate direction of expanding blastoderm.



the egg itself appears to be determined by the original orientation of the egg within the ovary. It is thought that the part of the ovum nearest the inflowing ovarian blood supply develops the highest metabolic rate and thus becomes the high point of the axial gradient. This end becomes the animal pole of the egg and hence the future head end of the organism. The orientation of the organism is thus determined by the stimulus of its position in the ovary.

The lateral and dorso-ventral orientation is also the result of external influence. The point at which the sperm enters the egg marks the meridian in which the dorso-ventral plane will lie, dividing the animal into a right and a left half, and becoming the mid-ventral region. The opposite side becomes the important mid-dorsal region, where the *blastopore lip*, source of such structures as the notochord, myotomes, and nephrotomes, is formed. Thus the broad outline of the organism is pre-formed in the uncleaved, just fertilized egg, and is instrumental in the unfolding of the potentialities in the genes of each cell of the organism.

Since all the cells of the embryo are derived from the original zygote by mitosis, the nuclei of all cells should be equivalent and so carry similar gene complements. And if genes are the hereditary determiners, as the evidence indicates, all cells should be equal in potentiality, should in fact be totipotent, since the zygote gives rise to the entire organism. The puzzling question why cells then differentiate in such a variety of ways has been partly answered by what we know of the cytoplasmic gradients within the zygote.

Experiments further increase our insight into developmental mechanics. If each new cell (blastomere) of the early embryo has the same nuclear structure as the zygote, why could not each one give rise to a complete organism? If a single blastomere is separated from the other three in the four-cell stage of a sea urchin embryo, it will produce an entire, but miniature, organism. At more advanced stages this is no longer possible. Blastomeres of various eggs, such as those of the sea urchin, *Nereis*, and even the frog, show this totipotency in

another significant, if perhaps less decisive, manner. If flattened between glass plates during several cell divisions and then released, the embryo will regain its spherical shape, but as it does so various blastomeres become displaced from their normal positions. Even so, the embryo will develop normally, thus showing that blastomeres which under normal conditions would have produced one tissue, upon displacement can produce some other. Finally, if the undivided but fertilized egg of a newt is constricted by a hair loop until it almost separates, with one part containing the entire nucleus, the nucleated half alone will undergo mitosis. If the loop is loosened somewhat later, one of the many nuclei now present in the dividing half may be allowed to slip across into the non-nucleated side, whereupon the two portions may be completely severed by once more tightening the loop. Even in cases where sixteen nuclei had formed before the loop was loosened, any nucleus whatever of those sixteen is still capable of directing the development of an entirely normal though somewhat smaller larva, from the half originally enucleated.

On the other hand, a single cell removed from an older embryo, or from a mature animal, will not produce a new organism, even though conditions are such that it can continue to live and grow. At best it will produce more cells of its own kind. What then happens to cells, or to their nuclei, to limit their potentialities? When does it happen? And why do cells differentiate into specialized tissues when they remain within the cell complex of which they are a part?

Much light has been thrown on questions of this sort by experimental mutilation, tissue cultures, and cell transplants or grafts. If part of the animal pole in a blastula of a sea urchin or newt is removed, ectodermal cells become reoriented in closing the gap. As a result, fewer cells take part in the invagination of the gastrula, and cells that normally would have been invaginated to produce endoderm become part of the ectoderm. Still a normal larva results. But when the same operation is performed on a gastrula, the endoderm can no

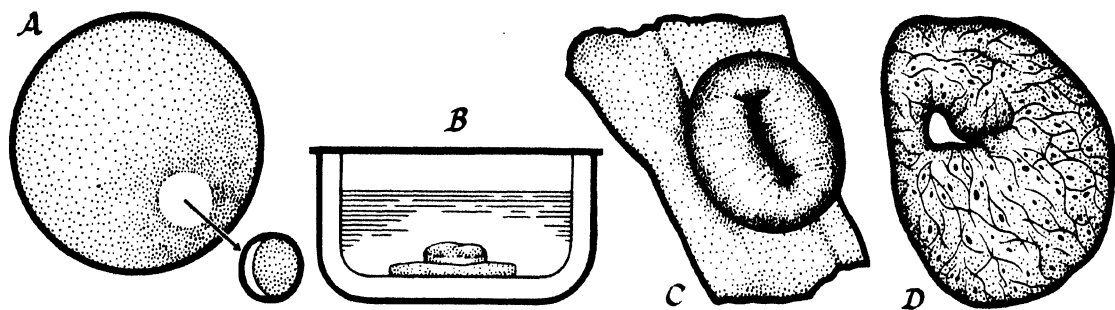


Fig. 398. A. A piece of ectoderm from a young gastrula is laid on a piece of dead material from another embryo. B. The piece of ectoderm has formed a nerve tube, (C), and its section shows the formation of nerve tissue (D). (After Holtfreter.)

longer be converted into ectoderm. The endoderm still retains considerable plasticity, however, since removing a segment of it from the gastrula does not prevent the formation of internal structures entirely normal, though somewhat reduced in size. Thus the changes in cells which limit their potentialities are progressive, for even after endoderm cells can no longer become ectoderm, they can still pinch hit for each other, producing structures normally produced by those that have been removed. The relation of a given cell to the cell complex determines what that cell is to become.

These conclusions are further substantiated by the startling results of tissue cultures. Kidney tissue from a mouse grows as undifferentiated embryonic tissue if cultured by itself, but if a bit of connective tissue is added to the culture, the kidney tissue differentiates into tubules! On the other hand, presumptive eye material taken from a late gastrula will produce eye cells, whatever part of the embryo it may be transplanted to, and despite the fact that there is no visible evidence of previous differentiation in the tissue. Thus it appears that differentiation and limitation of cell potentialities are not necessarily autonomous in the cell, but may be functions of its relation to the other cells of its environment. Further, differentiation may originate as an invisible change which is nevertheless permanent and endures even under later abnormal conditions, as in the presumptive eye material.

The differentiating effect of some cells upon others does not appear spontaneously in scattered regions of the embryo, but is an influence

that spreads from a center to peripheral regions, and it has been tracked down in newts and frogs to the dorsal lip of the blastopore. This is a "master region," and it induces cells to differentiate into the axial embryonic structures, the nerve cord, notochord, myotomes, nephrotomes, eyes, and ears, even if later transplanted from its normal position. This region is an *organizer*. But from what does this area — which after all is but a collection of cells like the rest of the embryo — obtain its peculiar power? Any piece of ectoderm, transplanted to this site early enough and then removed to another selected at random, displays the same organizing power. This power is not, to start with, a property of the particular cells of that region, but is a product of the region itself. The total effect of a group of undifferentiated cells — the embryo — initiates an organizing power or substance within a localized group of these cells.

The nature of this organizing influence is suggested by experiments in which isolated pieces of tissue are placed in varied relationships with each other. A sheet of prospective ectodermal tissue, which if isolated produces only ectoderm, will, if brought into contact with a bit of young neural plate or dorsal blastopore lip, become a neural tube with characteristic neural structures, and it will do so even if the neural plate fragment is first killed by heat (Fig. 398). The organizing influence, therefore, is probably a hormone which survives the death of the tissue that produced it.

Thus, the nature of the forces which form the organism begin to be intelligible. Various po-

tentialities lie within the single cells, but no cell, beyond the early cleavage divisions, functions autonomously. No cell is capable of independent differentiation, though factors within it determine its potentialities. The developing organism may be compared with the school-age portion of a community. The school is the organizer, and in it, the plastic units, the children, become differentiated and specialized. At an early age these units may be placed in special schools to be molded to their pattern. But as specialization proceeds, pliability decreases.

Similarly, the cell complex fits the totipotent cell into a special mold, but the molding is in turn the work of the other cells of the community. An isolated, undifferentiated cell fails to differentiate, although potentially it can do so. But in the normal environment of its fellow cells, it differentiates into one of the many special types within the range of its gene potentialities, depending on its chance position.

The concept of the gene as a specific catalyzing agent that produces specific results only under specific conditions explains a good deal. These gene specificities are limited and precise. Each gene, probably, as a rule, by controlling the presence of a certain enzyme, catalyzes certain physical and chemical activities within the cell, but only at a certain time and under specific chemical and physical conditions, which in turn are determined by the outer world and by the position of the cell within the organism. If these conditions are changed beyond a point of tolerance, these genes may produce different effects or may become ineffective, while others assume decisive roles.

Later Development

After the first steps in differentiation, which set the basic pattern of the organism, further development is largely shaped by the stresses and strains incident to functioning. Blood vessels, first "roughed out," are modified by the degree and direction of the flow of blood and by pressure within them. Thus a segment of vein transplanted to an arterial position becomes an unmistakable artery. Bone spicules

orient themselves for maximum strength. Nerve cells appear to be guided in their migrational growth throughout the organism by electrical gradients. Those in tissue cultures orient themselves to grow along the line of flow of an electrical current passed through the culture medium, but they grow at right angles to a wire carrying a current, suggestive of the way motor nerves branch off from the spinal nerve cord. During all these processes, chemical coordinators remain of great importance, so that by contact through the blood stream, tissues far from each other function in concert. In this connection, it will be helpful to recall the growth hormones and sex hormones (pages 409-416).

It must not be forgotten that the relation of the organism to its environment plays a dominant role in development. The dependence on specific environmental conditions becomes strikingly apparent if these are even slightly changed. Thus the larva of a sea urchin raised under abnormally high temperatures does not invaginate to produce a gastrula, but grows an everted alimentary canal. Lack of calcium in the sea water causes the blastomeres to separate, while lack of potassium prevents the larval skeleton from developing. In the fish *Fundulus*, paired eyes are transformed into one median, cyclopean eye if magnesium chloride is added to the sea water.

From beginning to end, the unfolding potentialities of an organism represent a complex interplay between genes and cytoplasm, between each cell and its environment within the organism, and between the cell complex and its outer environment. Normal structure results when normal genes produce their effects under normal circumstances. Because of continually changing conditions within a developing organism, the activities of any given cell change as the organism unfolds, although the gene complement is constant, thus enabling the cell to play those different roles for which it has been selected at each stage. To see the organism in perspective, we must then view it not as three-dimensional only, but as a changing mechanism moving also in that fourth dimension, time.

Vertebrates in the Water: Fishes and Amphibia

The Antiquity of Fishes

Fossil records tell us that, like all other higher forms of life, vertebrates originated in the water, and that these first vertebrates were fishes. Bits of real bone deposited in strata identified as having originated in the Ordovician Period, over 400 million years ago, represent our first tangible evidence of vertebrates. The nature of these fragments, and their identification as real bone, give evidence that these first known backboned animals must have had a long history of vertebrate evolution behind them, but its exact course is still shrouded in mystery. Paleontologists tell us that these fragments appear to have been carried from the upper reaches of streams into a bay, there to become fossilized. These first known vertebrates, then, did not inhabit the ocean, but appear to have evolved in fresh water, a fact which will assume further significance when we attempt to reconstruct the emergence of the first land vertebrates.

The first vertebrates well represented in fossil deposits, and today remarkably well-known anatomically, are certain *ostracoderms* (Gr. *ostrakon* = tile, *scale* + *derm* = skin), especially of the order *Osteostraci*. An osteostracan today would look like a queer fish, but it would be indisputably a fish. Heavily sheathed in an armor of fused plates and overlapping scales, these creatures were usually not much larger than an average-sized goldfish. Though fish-like in appearance, their anatomy was quite unlike that of most modern fishes, for they lacked certain structures now common to most, and reveal others which in most modern fishes are vestigial. Their heavy armor was evidently a protective adaptation against formidable in-

vertebrate enemies, chief of which were probably the eurypterids, the giant water scorpions. Peculiar, heavily innervated organs located in the heads of some of them appear to have been capable of emitting an electric shock, immensely valuable against attackers, and seem to have been much like those found in the electric eel and torpedo of the present day. The eyes of these quaint fishes were close together near the top of the head, presumably an adaptation to life on the river bottom, and between them there appears to have been a third, or pineal eye, preserved in modern vertebrates only as a rudiment of doubtful function. These creatures were jawless, equipped only with a small nuzzling mouth, and their appendages, where present, were but indifferently developed. In their ears they had but two semicircular canals instead of the three of most modern vertebrates, and a single median nostril opened out near the top of the head.

THE CYCLOSTOMES

Between Old and New

Among the wealth and variety of modern fishes, only the lampreys, which are cyclostomes, approach the osteostracans in their basic anatomy, and even these are completely outwardly dissimilar to the earlier forms (Fig. 399). Unlike osteostracans, the eel-like lamprey has no armor — indeed, it has not a single bone in its body. But its lack of jaw and appendages, its two semicircular canals instead of three, its single nostril, its nerves and blood vessels, as well as the great similarity of the brain, with its pineal organ, closely ally it with the extinct osteostracans. Some of the features of the cyclostomes are, no doubt, degenerative



Fig. 399. Sea lampreys, the closest among modern fishes to primitive types. Note gill slits behind the eyes.

changes resulting from their semi-parasitic mode of life, for lampreys prey upon fishes by attaching themselves with their round, tooth-studded mouths, which they use as suckers, while their rasp-like tongues drill into the flesh of the victim. The cartilaginous skeleton of the cyclostomes, once considered primitive, is now thought to be a degenerative change, as are the poorly developed eyes possessed by some of them. But on the basis of our knowledge of the osteostracans, most of the other peculiar features of the cyclostomes listed may be classed as primitive. Thus, despite their specialized and degenerative changes, their primitive features place them at the very bottom of the vertebrate evolutionary ladder.

Larval Affinities with Lower Chordates

Since the cyclostomes appear to be the most conservative members of the vertebrate class, a study of their embryology and early development should reveal clues leading to still more conservative invertebrate forms. In this we are not disappointed. The larva of the lamprey *Petromyzon* is so different from the adult that it was formerly thought to be a distinct species, was given a separate name, and is still known as the *ammocoete larva*. In its structural characteristics, this larva is strikingly and suggestively like *Amphioxus*, and like certain tunicates, too. It is a slender worm-like creature

with poorly developed eyes hidden under the skin, and without a trace of the special rasping mouth of the adult. Like *Amphioxus*, it burrows in the mud and obtains food from suspended particles which it whirls into its mouth to be filtered. In the throat is a ventral ciliated groove, precisely like the endostyle of *Amphioxus*, and in both creatures this groove forks at the anterior end, bends towards the dorsal wall of the pharynx, and leads into a ciliated groove which guides food particles back into the stomach.

After two to four years of larval life on the river bottom, there is a swift metamorphosis lasting but a week or two, and the ammocoete larva becomes transformed into the adult. Its eyes enlarge and move toward the surface, the lips grow enormously and develop their horny teeth, and the reproductive structures mature. The endostyle pinches off from the digestive tract and becomes glandular, to form the characteristic thyroid gland of a vertebrate. Thus, before our eyes, we may witness the transformation of an amphioxus-like chordate into a real if primitive vertebrate. Our mind's eye, baffled by the curtain of obscurity that time has thrown over the antecedents of the osteostracans, now sees beyond them. It sees as the ancestral chordate a small, segmented, and all but headless worm-like creature, its body stiffened by an elastic notochord, the

forerunner of the vertebral column which gave the vertebrates their name.

THE FISHES

The term "fish" is rather a loose one, and although we may call the cyclostomes fishes, the term is more properly applied to higher forms. With the relationship which has been established between the earliest-known vertebrates and the most primitive of modern ones, we would be led to expect a further neat evolutionary sequence from these to the higher forms. But in this we are disappointed. The osteostracans and allied forms are too highly specialized in their own way to be considered ancestral to any of the many forms of modern jawed fishes. Vertebrates of which we have but the most fragmentary knowledge were known to have existed in the Ordovician, and these fragments make it appear likely that highly developed vertebrates may have existed even in the Cambrian Period, a full 100 million years earlier. So it is in this nebulous past that side by side with the jawless osteostracans there evolved related ancestral forms of the jawed creatures which today form the great majority of living fishes, and indeed of all vertebrates.

The Cartilaginous Fishes

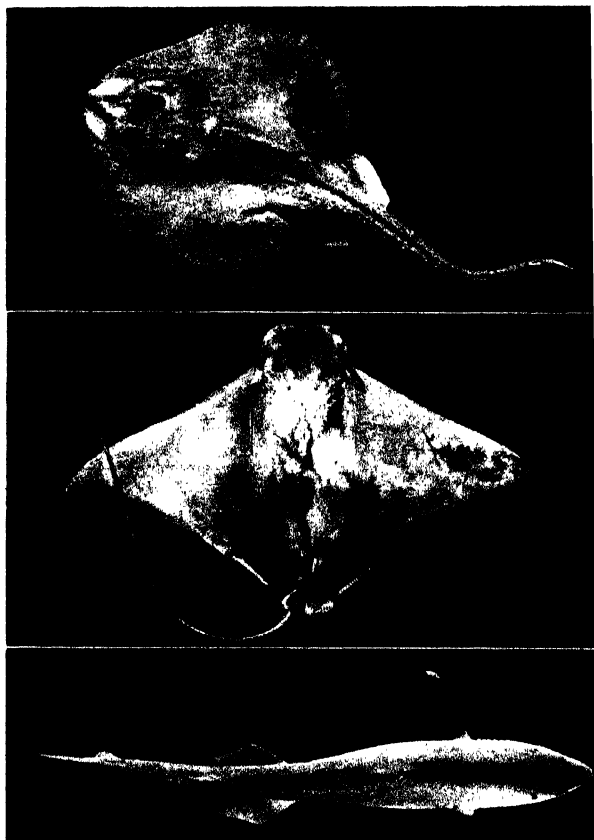
Modern fishes fall into two quite distinct classes, the cartilaginous fishes or *Chondrichthyes*, and the bony fishes or *Osteichthyes*. The cartilaginous fishes are the sharks and shark-like forms, such as skates and rays (Fig. 400), and it is true that they have no bones. Their ancestors did, however, and the earliest shark-like fishes, the so-called spiny sharks (*Acanthodia*), were well armored. Spines and scales typical of these fishes abound in Silurian deposits. Noteworthy is the variation in numbers of paired appendages in these early fishes, some having as many as seven pairs. The orthodox two-pair system of present-day vertebrates had not yet evolved, and it was here that evolution was determining that we were eventually to have but two arms and two legs — instead, perhaps, of half a dozen or so apiece. The

jaws of these early spiny sharks are still obviously primitive, and they clearly reveal their origin from modified gill-bars. The teeth are obviously modified and enlarged skin denticles (placoid scales) covering the infolded skin of the lip.

One does not have to be an ichthyologist to distinguish between cartilaginous and bony fishes, for each clearly reveals characteristic external features, most obvious of which are the gill slits. In virtually all cartilaginous fishes, five or more of these appear as separate openings. In the bony fishes there is a single flap-like covering over all the gill slits.

Modern sharks (order Selachii) range in size from the gigantic but harmless whale shark, which reaches a length exceeding seventy feet, and the swift forty-foot white shark, reputed to be a man-eater, to the small coastal dogfish (*Squalus*). Among the rays (order Bato-

Fig. 400. Cartilaginous fishes. Reading down: Prickly skate, Uyliobatid ray, and spiny dogfish.



dea), the terrifying devil-fish, or *Manta*, may measure twenty feet across its kite-shaped body and reach a weight of several tons. Flapping through the water with great lateral fins, it resembles a monstrous bat. Its reputed habit of leaping out of the water, especially when annoyed, and then allowing its massive weight to fall flat onto the water, makes it dangerous game to hunt from an open boat with harpoons. The sting-ray of tropical waters, with its poisonous tail-barb, also belongs to this order. The rare, odd and obscure Chimaerae or rat-fishes are also grouped with the cartilaginous fishes, but they appear to have had a long and independent evolutionary history.

Despite their wide variations in form and size, the cartilaginous fishes have not been notably successful in adapting themselves to widely different modes of life or environment, and their numbers today are relatively small. None have ever shown any tendency toward migration to the land. None have ever taken to the air, and they show a much smaller range in size than do most higher vertebrates. Perhaps their most striking divergence is the ability of some of them to produce living young by a placental type of uterine nourishment, otherwise found only in the highest vertebrates. But this mechanism is different in structure from that of the placental mammals and is an independent product of evolution. The many apparently primitive structural features — though some must be considered degenerative — such as placoid scales, cartilaginous skeleton, separate gill openings, poorly braced and fused jaw structure, poor brain development, and others, make these relatively conservative fishes an instructive introduction to the higher vertebrates.

The Dogfish, a Representative Cartilaginous Fish

The digestive system of the dogfish is typical of the vertebrate digestive system generally. It has the usual sequence of differentiated regions and organs, including a liver and a pancreas. The most unusual feature is the spiral valve of the intestine. This is a structure, rather like a spiral ramp in plan, by which the

intestinal surface is increased. The circulatory system follows the single closed pattern and is of interest because of its simplicity and its similarity to that of *Amphioxus*. The system differs little from that of the bony fishes, but the heart is little more than a bent, chambered tube, not unlike that found in a young mammalian embryo. Respiration is by means of gills, basically much like those of the bony fish, but opening to the outside through separate gill-slits. Such gills represent a considerable advance over the primitive gill pouches of the cyclostomes (Fig. 383). Excretion, as in bony fishes, is by a functional mesonephros (page 435), the anterior portion of which also serves as the sperm duct in the male. Derivatives of the mesonephric ducts serve as oviducts and uterus in the female.

The brain of the dogfish is more highly developed than that of the cyclostomes, and its olfactory lobes are particularly prominent (Fig. 362). Little is known concerning the chemical system of coordination, the endocrine system, beyond the fact that the important endocrine glands common to all vertebrates are present.

The Bony Fishes

The bony fishes are generally divided into five large orders, but some of these show only a slight relation to others within the group. This is another way of saying that the class of the bony fishes has been made a sort of catchall into which some superficially similar vertebrates living in similar environments have been placed for the sake of convenience. Actually this is of no great consequence, since by far the greater number of fishes belong to but one order, the *Teleostei*, or "true" bony fishes. Although the bony fishes trace back well over 300 million years, the teleosts are relative newcomers and did not appear in force until the end of the Jurassic Period, about 120 million years ago. Their comparative recency is sharply accentuated by the fact that at the time of their appearance, a progressive branch of lobe-finned fishes (*Crossopterygii*) had not

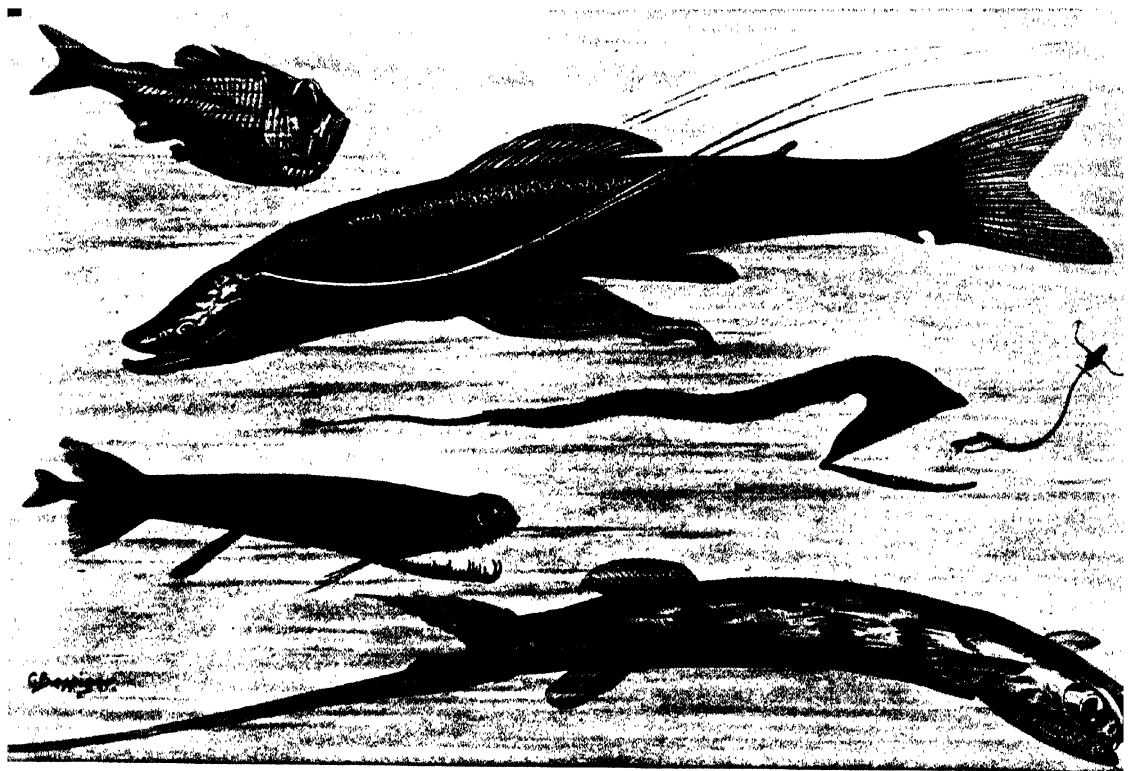


Fig. 401. Abyssal fishes show strange adaptations to life in the dark: large eyes, luminous organs, gaping mouths, grotesque jaws, and formidable teeth.

only given rise to the amphibians and through them to the great Jurassic reptiles, but that these had already reached the peak of their glory!

Early Bony Fishes. The teleosts form the bulk of all the fishes that the average person ever sees. They fill our rivers, seas, and oceans, and outnumber all other aquatic vertebrates overwhelmingly. Like the cartilaginous fishes, the bony fishes trace back to jawless progenitors of the jawless cyclostomes. The first known representatives of the bony fishes date back to the Devonian Period, and they seem to have lived at about the same time that the first sharks left their skeletons to be fossilized. These first bony fishes, like the contemporary sharks, were grotesquely armored in heavy plates of bone, and probably through the same cause — adaptive protection against the great eurypterids.

Strangely enough, most of these early bony fishes were equipped with sac-like air-breathing structures, or lungs. A severe climate, with alternate floods and droughts, may have pro-

duced conditions similar to those still existing in some modern tropical climates, where lakes and ponds are periodically reduced to foul, stagnant pools, devoid of oxygen. Under such conditions, an animal entirely dependent on oxygen dissolved in the water has a poor chance of survival, while a premium is attached to the ability to make use of atmospheric oxygen. It is under such tropical conditions that the lung-fishes of today still exist, and it was probably under such conditions that there evolved the first bony fishes with lungs sufficiently well-developed to enable them to survive a short overland trip from their vanishing pool to the next larger one. Parallel development and strengthening of the paired appendages would have had further selective value. Thus the fresh-water habitus of the early bony fishes led the way to the amphibians, such as the salamanders and newts. But few of the earliest lunged fishes appear to have been capable of such a venture, and most of them seem to have found other adaptive measures, or to have drifted down the rivers to the oceans, where



Fig. 402. The flying fish, *Exocoelus*.

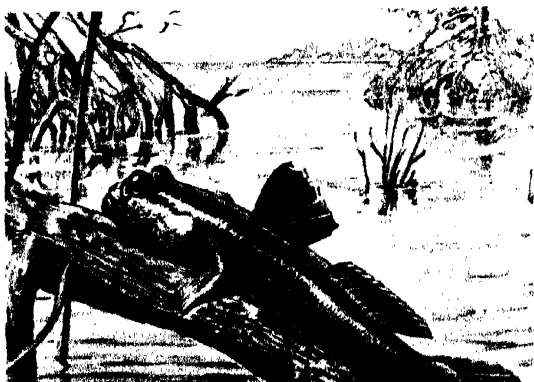
lungs were unnecessary in their original form and were modified and transformed to serve as hydrostatic organs, the swimming bladders. In the ocean, adaptation appears to have been easy for the bony fishes, since soon after their first records were deposited, there began a great spreading of these fishes throughout the oceans of the world. In the course of this process, the old ancestral armor, now apparently a detriment rather than an asset, was shed. The evolution of the modern bony fish was well under way.

Characteristics of Bony Fishes. The teleosts are characterized by their thin, rather transparent and strongly overlapping scales, and their almost completely bony skeletons. In contrast with the older lobe-fins, their appendages have but a short fleshy base, while the main surface is stiffened by supporting rays, or in higher forms, by spines. The success of the teleost pattern is overwhelmingly proved by their vast numbers and by their diversity of form and mode of life. They range in size from the inch-long mosquito fish (*Gambusia*) to two-ton giants like the ocean sunfish. They assume all conceivable shapes, each apparently well adapted to a special environment or feeding habit. There are snake-like, crevice-loving rays and eels; fishes that feed along the ocean bottom and have a flattened ventral surface, like the trunk fish; and bizarre weed-dwellers like the seahorse (*Hippocampus*). But the majority have evolved the streamlined form best adapted for rapid swimming, the torpedo shape so well exemplified by the mackerel.

The teleosts range from brooks and ponds to the abysses of the ocean. Some, like the flying fish (Fig. 402), venture on flights of several hundred feet into the inhospitable atmosphere. The odd *Anableps tetraphthalmus* ventures onto the mudflats to bask in the sun. It is a surface swimmer, and each of its eyes is divided into two sections, one for vision below the water and the other for vision above it. The comical mud-skipper, *Periophthalmus* (Fig. 403), has also begun to make itself at home on land, and has even learned to clamber about on mangrove roots. A labyrinthine air chamber above the gills makes it possible for this fish to utilize atmospheric oxygen. Abyssal fishes, restricted to the complete and eternal darkness of the ocean depths, refugees from regions of greater competition, show grotesque adaptations in the form of gaping mouths, huge eyes — or the complete lack of them — and fantastic arrays of luminous organs (Fig. 401). The success of the teleost pattern is amply demonstrated.

Similar diversity is found in the reproductive habits of the bony fishes. Some, by the "shot-gun method," scatter their eggs and sperm into the water in vast quantities, while others build nests and carefully nurse and protect their relatively few young. In still other types, the young are born alive. Among the seahorses, the male takes over the duties and inconveniences of pregnancy by swallowing the eggs produced by the female and storing them in a special brood pouch where the embryos are even nourished by a special exudate.

Fig. 403. The mudskipper, *Periophthalmus*. A fish that spends much of its time on land, skipping about the mudflats in search of insects. The specimen shown inhabits a mangrove swamp.



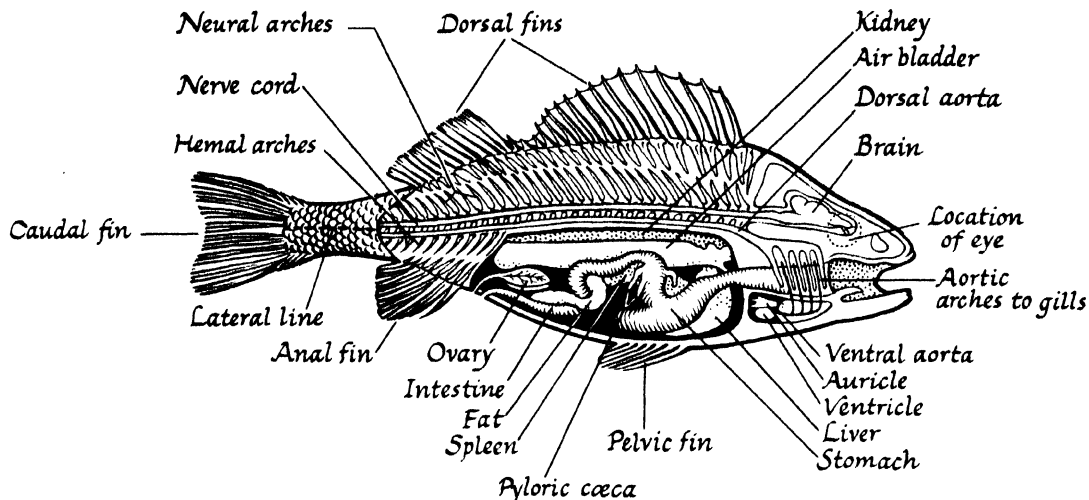


Fig. 404. Diagram of a bony fish (perch), showing the fins (except pectoral) and the essential internal organs. (Modified after Woodruff.)

Evolution in fishes has taken many surprising turns, but they have shown very little brain development. The brain of the bony fish (Fig. 362) is indeed more highly developed than those of cyclostomes and cartilaginous fishes, but the development is restricted primarily to those centers associated with the sense organs — especially the optic lobes — and with coordination (the cerebellum). Centers associated with learning or reasoning ability (the cerebrum) are but rudimentary. In these aquatic vertebrates we find in primitive form many of the prerequisites that, if steered into other channels by supplementary mutations, might have made possible the transition to landlife, and which in other aquatic vertebrates did just that.

VERTEBRATES INVADE THE LAND: THE AMPHIBIANS

Living organisms are opportunists. They can never deliberately change their heredity to meet new environmental conditions; they can only trust to good fortune in exploiting in a manner suitable to their needs whatever qualities they already possess. Before vertebrates could crawl out of the water they needed the support of a bony skeleton, limbs with more strength and stamina than fins, and lungs with which to breathe air. Full conquest of the land

demanding even more — reproduction by laying eggs in the water had to be eliminated and a skin that would protect against drying out had to be evolved. A successful land animal would require all of these things, though for a beginning in a non-competitive field, it might get by with less. The acquisition of one or two of these alone would not suffice.

We do find that one or another of these was evolved, often repeatedly, by animals otherwise wholly unsuited for land life. The sea robin, a fish, has evolved queer legs, but no other feature to recommend it as a candidate for land life. The mudskipper has unusually strong fins upon which it can actually support the front half of its body, but its other adaptations to land life are strictly makeshift. Various fishes, notably the sharks, have replaced the laying of eggs in the water by a live-bearing mode of reproduction, which, had it been linked with other adaptations for land life, might have given them a wonderful start as land dwellers. Incredible ages ago the lungfishes evolved suitable lungs and a makeshift mucous secretion to protect themselves against drying, but here their luck ran out. They can survive limited droughts, but if their pond stays dry too long, they are doomed, for locomotion on land is quite beyond their best efforts. They have waited in vain these millions of years for

further, necessary mutations, and today they are confined to a few restricted and shrinking regions in scattered parts of the tropical world.

That any creature should have experienced the good fortune of combining in its body all of the essentials for land life seems almost incredible, and yet, no more so than the entire spectacle of evolution itself. The conservative lungfish of today, in its form and habitus, displays graphically the manner in which the first venture onto the land took place. With a wholly adequate lung, it conservatively retains its gills; but when the pond in which it lives dries up, the lungs carry it through. Had the mudskipper evolved the lung of a lungfish, or had the lungfish acquired sturdy flippers like a mudskipper, an amphibian would have been created. It is in just such a manner that somewhere in the mid-Devonian the first amphibian did originate, though the first known footprint of such an animal was not recorded until the end of that period.

For the earliest amphibians, home was still in the water, and land was merely an emergency viaduct to a new home should the old one fail. At the beginning of the next period, the Carboniferous, the land was already lush with vegetation, but this offered little to the first amphibians, whose carnivorous ways were inherited from their carnivorous fish-forebears. What arthropod life had followed the plants onto the land could have been of but little value to the lumbering, squat-legged and belly-sliding, first amphibians. They had to return to their home element for food — and to this day the amphibians remain carnivorous.

The Carboniferous *Keratopetion* (page 128) exemplifies the early amphibian. It did not exceed two feet in length, and in its general appearance it was still fish-like. As in the fishes, the body was long and slender, the tail well developed and heavy, and the appendages relatively weak. The salamanders and newts of today closely resemble these ancients, although in the reduction of their skeleton, especially of the skull, these modern amphibians are distinctly degenerate. In such a close similarity between amphibians and their an-

cestors among the lobe-finned fishes, even to their completely fish-like larval development, we also see the cause of their failure. The amphibians are, and always were, a makeshift sort of animal. They are fishes superficially adapted to spells of life on land. It was to an aberrant offshoot of these early and still unspecialized amphibians, the reptiles, that full conquest of the land was to fall.

The Modern Amphibia

Once the unchallenged inhabitants of the land, modern amphibians are now but a struggling, conservative remnant of these originally progressive animals. With a few exceptions, they are small, defenseless creatures, narrowly limited in their habitat by the imperfections of their anatomy and physiology. As a result of innumerable combinations of adaptive variations, some have become almost wholly terrestrial, while others appear to have given up the struggle and have reverted wholly to aquatic life. Today only the salamanders and newts (*Urodela*), the frogs and toads (*Salientia*), and the obscure "blindworms" (*Apoda*) represent this class.

Perhaps the most common feature of the amphibians is their moist, glandular skin, thin and soft and demanding a moist environment. With a few exceptions, to be noted later, amphibians lay their eggs in water, where they develop into gilled larvae, "tadpoles." They are generally quadrupeds, but the aberrant blindworms are legless. The adults generally have lungs, but some tailed amphibians retain their gills throughout life, while some small forms have lost both gills and lungs, and reverting to the level of a worm, breathe only through their skins. Internally they show modest improvements over many fishes, and perhaps the most significant of these are in the circulatory system.

The fishes have a simple two-chambered heart, but the amphibians have taken the first step toward acquiring the separate circulation of oxygenated and unoxygenated blood — toward separating the pulmonary and body

(systemic) circulations into the complete double system found in birds and mammals. That is, in the heart of the frog we see a complex but still makeshift mechanism by which the head and brain receive relatively pure oxygenated blood while the blood in greatest need of oxygen is shunted to the lungs (see page 462).

Primitive though amphibians still are, many of them are highly specialized in body form and habits. They are primitive in such structures as ears, kidneys, nervous system, circulatory system, and reproduction. But they are specialized in body proportions (as in the long leaping legs of the frog), in the shape and function of the tongue which serves as an insect snare, and in some of them, in peculiar adaptive changes of the primitive mode of reproduction of the class. Specialized, too, are the swimming feet of some, the vacuum-cup toes of others, and the webbed flying toes of still others. Since they are generally quite defenseless, it is perhaps puzzling that they should have survived at all. But with one or two exceptions they are small, and aided by protective coloration they lead hidden and inconspicuous lives. The frogs have added to this an explosive escape technique, for their long, powerful legs catapult them toward the safety of the water at the slightest hint of danger. Toads have evolved poisonous skin glands on the neck and head which appear to make them so distasteful that most animals leave them strictly alone. They are not, however, poisonous to touch, nor do they "cause warts." Beyond these few simple mechanisms, however, amphibians are defenseless, and their most potent bid for survival lies in their fecundity. Generally herbivorous as larvae, the adults have all remained insectivorous or carnivorous, and the enormous potential food supply of land vegetation remains closed to them.

Adaptive Divergence in Amphibians

Despite the striking backwardness of amphibians as a group, adaptive specializations have arisen with them, as we have seen. Besides such more conventional adaptations as protective coloration, unobtrusive habits of life,

small size, erratic movement and bursts of speed, and in some the development of poison glands, some astonishing specializations have been developed in reproduction and reproductive ways. Typically, amphibians lay eggs in gelatinous clumps or strings in ponds or streams. The gelatinous covering is a protection against loss by sinking into the mud and it makes them unattractive as food to most small animals. The tadpoles, however, are wholly unprotected, and in most species they die by the millions.

A few varieties, however, avoid this loss. The South American tree frog, *Hyla faber*, uses her hind feet as trowels and builds low earth dams at the edges of ponds, thus producing miniature private pools in which she deposits her eggs. In due time, rains break down the dam and allow the partially developed tadpoles to complete their growth in the pond. The Javanese flying frog builds a suspended aquarium for its brood. The foamy, sticky mass of eggs is pressed against the leaves of trees or bushes, and while the surface of the mass hardens, the interior liquefies. The young tadpoles swim about in this aerial cradle until a tropical downpour washes them to the ground and into larger pools, where they complete their metamorphosis.

The male obstetrical toad draws the strings of eggs out of the female (hence its name), and after fertilizing the eggs, it tangles the strings around its legs. The eggs remain so attached for four weeks, despite the otherwise normal land activities of the male. The gelatinous covering is sufficient protection against mechanical abuse and drying out. When the larvae are ready to hatch, the father returns to the water where, aided by his vigorous kicking, the brood quickly breaks out of the egg cases and disperses. Although the young are thus protected against predators for a time, there are other hazards, for egg packets are not infrequently lost and the larvae die because of their failure to reach water.

Other variations equip the amphibian to evade drought. The eggs of the Australian toad *Pseudophryne australis* are laid along the

margins of temporary pools, but are able to endure within the egg cases for several weeks beyond the time when they are ready to hatch, biding a needed rainfall. Still other adaptations help offset the limiting factor of an aquatic larval state, but these are frequently erratic and unbalanced. Thus a little frog (*Zooglossus seychellensis*) of the Seychelles islands in the Indian Ocean lays eggs under fallen foliage. The father remains with the eggs, which soon hatch into gill-less, but also limbless, tadpoles. The young work their way onto the father's back, where they adhere by a sucker-like mouth. Here, in moist air, they complete their metamorphosis, far from any pool or puddle, and with only their yolk-mass for food. This forms an interesting comparison with a small New Guinea frog (*Phrynxalus biro*), whose eggs also develop directly into lunged young, but not as an adaptation to land life, since the eggs hatch in mountain streams. Here this precocious development apparently has some selective value, for it enables the young to leave the stream before they are swept away by the current. In these two species, which are widely separated geographically, similar mutations adapt the organisms to radically different environmental conditions.

In numerous other cases the young either skip the gilled larval stages or pass through them while protected within their egg cases or in brood pouches of either the male or the female parent. *Hylodes martinicensis*, a frog of the West Indies, lays its eggs under moss or stones, and these develop without metamorphosis into small frogs equipped with a large vascular tail that serves as a respiratory organ. The Surinam toad distributes its eggs over its back with a protrusible ovipositor (Fig. 405). Here they sink into depressions like pockmarks which become sealed over. In these individual chambers the gilled larvae undergo metamorphosis and emerge as air-breathing toads.

The female of the pouched frog of Ecuador (*Gastrotheca marsupiala*) bears a brood pouch upon its back in which the eggs develop to the larval stage, at which time the mother deposits

them in a pond. But with *Gastrotheca ovifera*, whose eggs and larvae are similarly stored, the larvae pass through their complete metamorphosis before being released. They produce a remarkable breathing organ, their gills assuming the shape of large round disks, richly supplied with blood vessels. These gills have been named *allantois gills* because of their assumed similarity in function to the *allantois*, an embryonic membrane of the higher vertebrates (Fig. 406).

The gradual transition from the oviparous to the viviparous mode of reproduction is strikingly illustrated in two closely related European salamanders, *Salamandra maculosa* and *Salamandra atra*. The former lives in the lowlands and lays its eggs in ponds. The egg membranes burst the moment the eggs are laid, and the fully formed gilled larva swims away, and may even feed only a few seconds after birth. The mountain salamander, *Salamandra atra*, far from pools or ponds, produces a number of eggs comparable to that of its low-

Fig. 405. The female of the Surinam toad, which incubates its eggs and carries the tadpoles through metamorphosis in lidded pockets on its back.



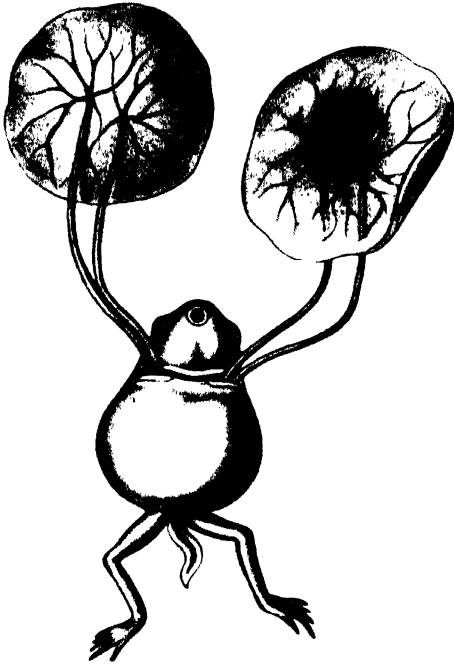


Fig. 406. Larva of *Gastrotheca ovifera*, as taken from brood pouch. Leaf-like structures are modified "allantois" gills.

land cousin, but only those nearest the exit of the uterus develop. The others disintegrate, and the two remaining larvae — one on each side — eat the liquefied yolk of their siblings and later even a bloody exudate of the uterine wall. Their gills are well developed during intrauterine life (Fig. 407) and appear to serve as an additional organ for absorbing soluble nutrients from the wall of the uterus. That is to say, they have what amounts to a placental form of nutrition, common only in the higher mammals. The gills later disappear, and the salamander is completely developed at birth.

As a final example, a grotesque and seemingly makeshift process deserves mention. In the gnome-like Chilean frog *Rhinoderma darwini*, the eggs are swallowed into a large ventral brood pouch by the male. Here the young undergo complete development. After their yolk supply is used up, they adhere to the walls of the pouch with their backs and appear thus to obtain nutrients from the circulatory system of the father. In due time, they are delivered through his mouth, fully developed frogs. We

are reminded of the analogous brooding of his young by the father seahorse.

These are but a few of the many adaptations among amphibians which contribute to their survival and which give eloquent testimony to the wide range of variations resulting from nature's shot-gun method of mutation. Many of the more bizarre variations are obviously of limited value, and we may well marvel that they persist at all. We may also wonder why, since viviparity occurs in some amphibians, this development did not lead to a further burst of evolution similar to that which gave rise to the many forms of reptiles. We may be reminded that a single successful modification is not likely to form a new and basically successful type. The amphibian development which led to the laying of large leathery eggs — that is, to the reptiles — has been coupled with other superior factors.

Mating and Development

Mating instincts vary in different amphibians, but in general remain at a rather low level of development. Frogs and toads show relatively little specialization in reproductive structures as well as in behavior. In the female, two large ovaries lie in a peritoneal fold ventral to the kidneys. At maturation, the ova are discharged into the body cavity, there to be picked up by the ciliated openings of the oviducts, the *ostia*. During their passage down the oviduct, a gelatinous coating is deposited around the eggs, and this swells upon contact with water to form the characteristic jelly-like coating. The testes of the male are two bean-shaped structures lying against the anterior ventral surface of the kidneys. Numerous short ducts, the *vasa efferentia*, conduct the sperm to the *mesonephric* duct, which thus serves for

Fig. 407. Embryo of *Salamandra atra*, the mountain salamander. Note the gills. These are resorbed before birth.



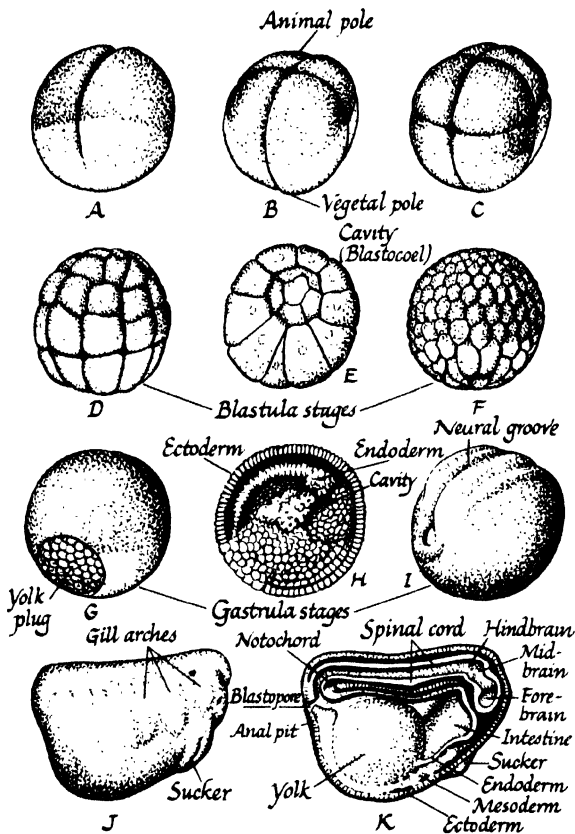


Fig. 408. Embryological development of the frog.

both reproduction and excretion — a primitive condition. Spermatic fluid is conducted to the common opening of digestive and urogenital tracts, the cloaca, and from here is discharged into the water.

Mating takes place in the water. Seasonal endocrine changes drive even the land-living toads to find ponds, where they engage in their chorus of trills, pipings, and grunts, their mating calls. In the males, a powerful clasping reflex causes him to grip a partner, once found, with his forelegs. In this there is little discrimination as to partners, and only the favorable reaction of the female eventually leads to pairing off. The male grips the female just behind her forelegs, clinging to her back, and stays in this position until the eggs are laid, a process apparently assisted by the pressure of his clasping arms. The male then releases seminal fluid

over the eggs, and fertilization is external. After the laying process, the eggs are abandoned and the parents quickly lose all interest in each other.

A somewhat different procedure is followed by certain newts. Here the male acquires a colorful mating costume, and his behavior during the mating season is such as to attract the attention of the female and elicit the proper response. Posing and strutting before the female on a level bit of pond bottom, he eventually produces a conspicuous packet of sperm. If all conditions are suitable, she picks up the packet with her hands and inserts it into her cloaca. It is noteworthy that such sperm packets are completely ignored if presented to a female in the absence of a courting male.

Within its gelatin capsule, a frog's egg goes through the standard pattern of cleavage (Fig. 408), except for modifications caused by the greater quantity of yolk stored in it. The first two cleavage furrows (A and B) are at 90° to one another, and four similar cells are produced. Thereafter cleavage is more rapid toward the animal pole until the asymmetrical blastula (E) is produced. Further infolding produces the considerably modified gastrula (H). The neural groove and the neural folds, beginnings of the nervous system, develop much as in *Amphioxus*, and establish the neural canal. The enteron or gut is still filled with unused yolk which is gradually absorbed. Soon after the basic vertebrate pattern is established, the young embryo breaks its egg-case and begins to swim freely in the water (Fig. 409). The larval mouth differs radically from that of an adult, for it is small, toothless, and equipped with a horny rim used for scraping algae from plants and rocks. The intestine of the tadpole is long and coiled, and thus provides the large capacity and length required for digesting plant food. In contrast, the intestine of the adult frog is short, as it is in carnivorous animals generally.

The young tadpole possesses no paired appendages, but does have paired external gills, later replaced by internal ones which then open to the outside through a single opening,

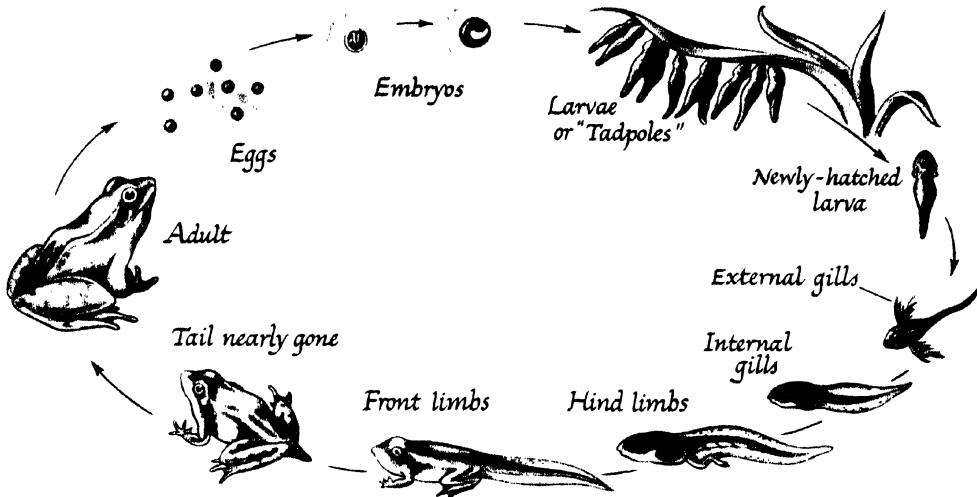


Fig. 409. The development of the frog from egg to adult.

the spiracle. Hind legs first make their appearance, but the front legs develop for some time under a skin fold, the *operculum*, which also covers the gills. At the proper time, a hole appears in the operculum and the foreleg comes through, much in the manner of an arm stuck through the arm-hole of a vest. This is an interesting bit of synchronization, for the hole appears at the proper time even if the leg bud has been removed. The larva is now ready for metamorphosis. Lungs develop to supplement the gills, the tail shortens, and the young frog begins to make frequent trips out of the water. The mouth becomes transformed into the typical wide frog mouth, the tail is finally resorbed entirely — it does not drop off — and the frog is complete.

The Bullfrog

Although highly specialized in certain skeletal and muscular features, the frog is a representative amphibian. In the bullfrog (Fig. 410), the large head merges with the body without any visible neck. A wide mouth reaching from ear to ear functions as an insect trap. Nostrils are dorsally placed, and the eyes are protruding mounds on top of the head, as in many animals that float in the water, even such widely separated types as the hippopotamus and crocodile. The body of a bullfrog is short

and bullet-shaped, stiffened by a welded skeletal framework which serves well for its projectile type of locomotion. The short front feet have four visible toes and the rudiment of a thumb, while the hind feet, retaining all the primitive five toes, are webbed.

The Skin. The skin of the frog is simpler than that of higher vertebrates. The outer horny layer of the epidermis is still only one cell thick, as in fishes, in contrast to the many-layered outer skin possessed by reptiles, birds, and mammals. But in the frog it is more resistant to drying than in the fishes, for instead of simple gland cells, the frog has multicellular glands, some secreting mucus and some, poison (Fig. 411). Chromatophores in the skin contain granules of pigment which nicely blends the animal into its normal background.

Fig. 410. The bullfrog, *Rana catesbiana*, largest of our frogs.



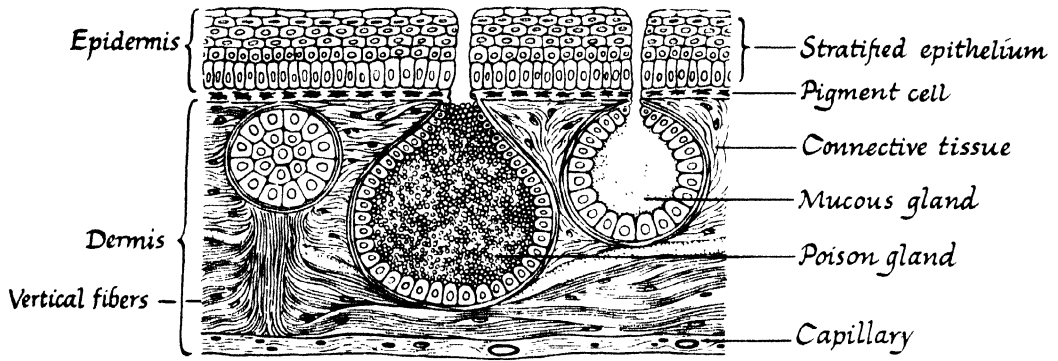


Fig. 411. Cross-section of the skin of the frog.

The Skeleton. The skeleton shows marked specialization (Fig. 412). The brain case of the skull is not much more than a tubular bridge running between the eyes. The primitive needle-like teeth are limited to the upper jaw. The backbone consists of nine vertebrae, of which the last articulates with a long urostyle, and by its lateral processes with the two elongated *ilia* of the pelvic girdle. Thus half the length of the axial skeleton consists of an elongated pelvic girdle, providing the rigidity needed for leaping and landing.

The Digestive System. The bullfrog has a

prodigious appetite and a digestive system to match it (Fig. 413). It is strictly carnivorous, and its menu includes worms and insects, fish, crayfish, small frogs, and even an occasional mouse or small bird. The prey is swallowed whole, and powerful digestive enzymes digest it, all but the bones, which usually pass through the system intact.

The Circulatory System. The circulatory system of the frog is intermediate between that of fishes and that of birds and mammals (Fig. 414). Where the heart of the fish has two chambers and that of birds and mammals has

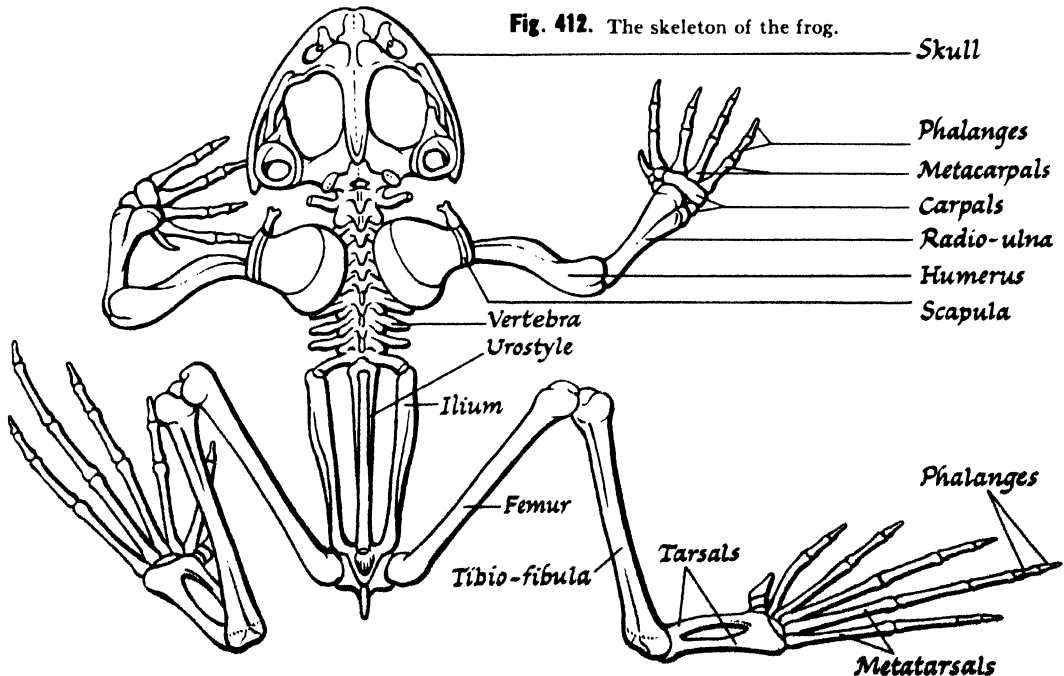


Fig. 412. The skeleton of the frog.

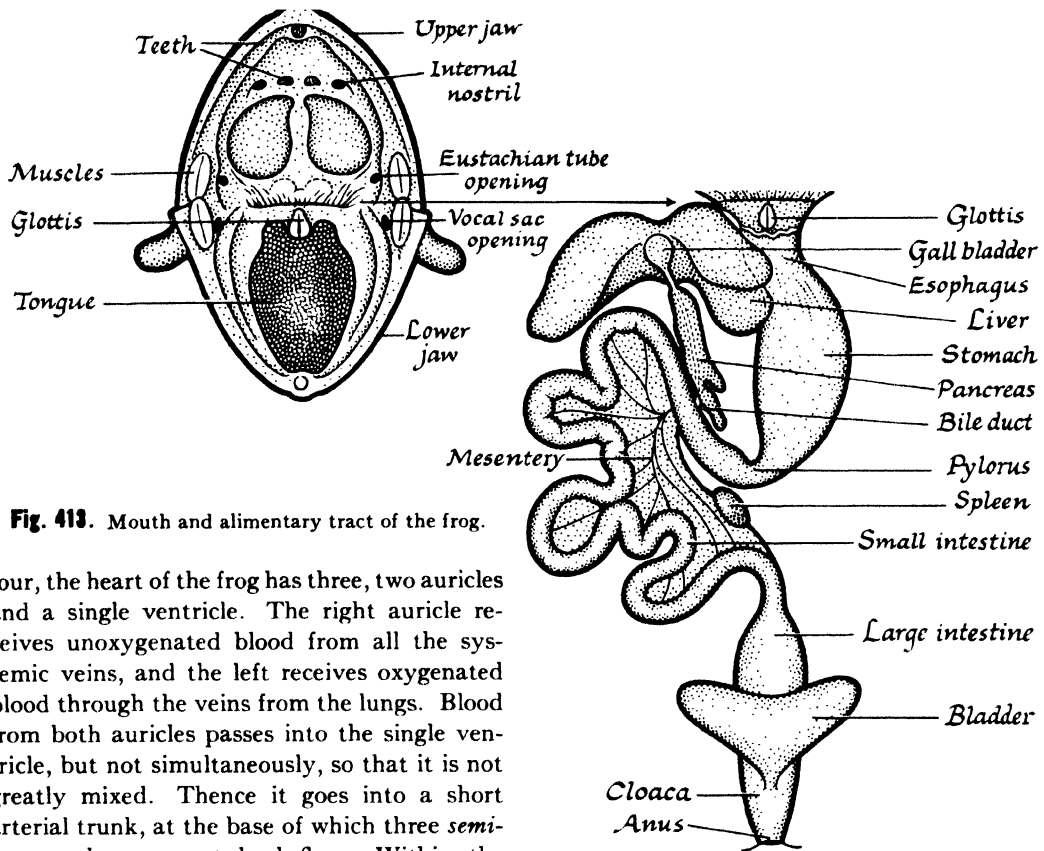


Fig. 419. Mouth and alimentary tract of the frog.

four, the heart of the frog has three, two auricles and a single ventricle. The right auricle receives unoxygenated blood from all the systemic veins, and the left receives oxygenated blood through the veins from the lungs. Blood from both auricles passes into the single ventricle, but not simultaneously, so that it is not greatly mixed. Thence it goes into a short arterial trunk, at the base of which three *semi-lunar valves* prevent back-flow. Within the trunk artery is a flap of tissue, the *spiral valve*, which automatically shunts most of the unoxygenated blood to the lungs while the rest goes to head and body. As the ventricle contracts, the unoxygenated blood from the right ventricle is pumped out first, entering the pulmonary arteries. As this new blood fills the capillary system of the lungs, the spiral valve is closed by back pressure, and the rest of the blood in the ventricle, mostly oxygenated, rushes into the systemic arteries, and passes to the brain and the rest of the body. Thus the heart of the frog achieves a fairly efficient distribution of the blood despite the fact that it has but a single ventricle.

Two *portal systems* are another feature of the circulatory system. The *hepatic portal* system conveys blood containing soluble foodstuffs from the digestive tract to the liver and thence to the heart. In the frog this system is much like that found in all vertebrates, including the mammals. It begins as a network of capillaries

in the intestine and other digestive organs. These capillaries merge to form the *hepatic portal vein*, which again breaks up into numerous capillaries and sinuses in the liver tissues, enabling them to handle the absorbed food-stuffs before there is any general distribution. These capillaries of the liver then reunite to form the *hepatic veins*, which feed into the *post-caval vein*, which carries the blood to the right auricle. Thus, unlike most veins, the portal vein begins in capillaries in the intestines and ends in capillaries in the liver. There is a similar system of two *renal portal veins*, which return blood from the legs and pelvic region and branch into capillary networks in the kidneys. The purified blood from the kidneys enters the *renal veins*, which also enter the great postcaval vein. The renal portal system is not found in higher vertebrates.

Respiration. Adult amphibians are air-breathers, but their breathing mechanisms are varied and not always as localized as those in

higher vertebrates. Some breathe through the skin only and others by means of a vascular mouth and throat lining, but most of them have lungs. The frog combines all three methods, though during its active summer life the lungs probably play the major role.

The mechanism of lung ventilation differs from that of higher vertebrates, however, for in the frog the air is really swallowed, whereas in reptiles, birds, and mammals it is "drawn" in. Some gas exchange occurs in the mouth and throat, but most of it takes place in the

lungs. These are still primitive, for their chambers are relatively large and have a limited surface.

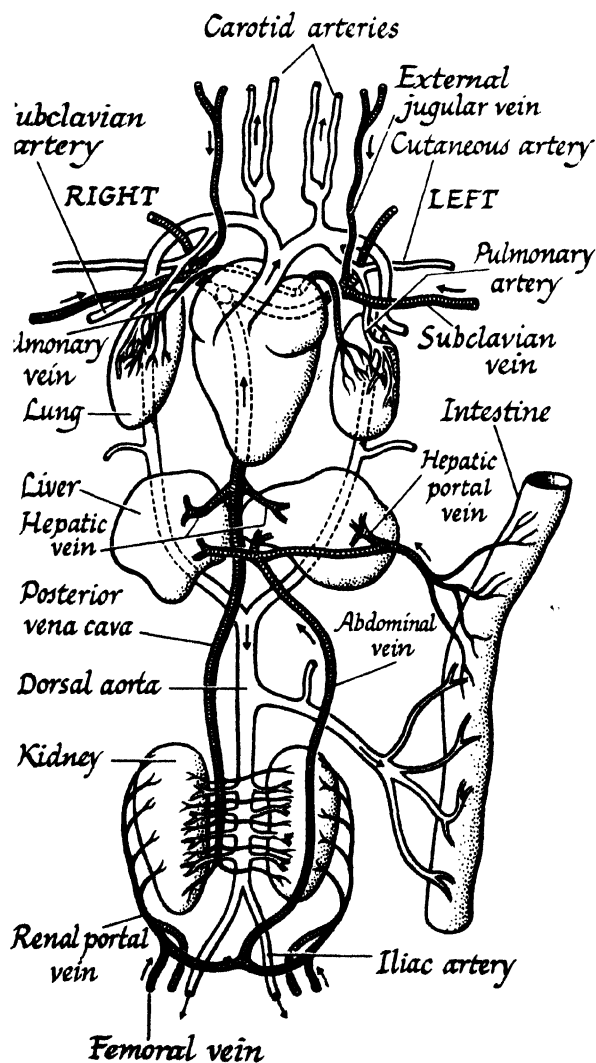
Excretion. The pronephros of the tadpole gives way to a mesonephros in the adult frog. In the male frog the mesonephric duct serves both as ureter and sperm duct, whereas in higher organisms the excretory function is taken over by the metanephros.

The Nervous System. The brain of the frog is still relatively undeveloped (Fig. 415). The functions and relative importance of the different brain regions can be experimentally determined by removing or destroying one at a time and observing the subsequent behavior. Little effect is noticed if the cerebral hemispheres are removed, since these show no organization into a cerebral cortex. Destruction of the midbrain destroys sight and the power of spontaneous movement, and increases the irritability of the spinal cord. Most of the responses of a normal frog persist even when the entire brain, with the exception of the medulla, is destroyed, but destruction of this portion causes death.

The cord of the frog is short and gives off ten pairs of spinal nerves (Fig. 416). Many of the animal's activities are coordinated by centers in the spinal cord, as is evident from the fact that a decerebrated frog is still capable of performing most of its normal activities. This also implies that there is relatively little intelligence involved in its normal behavior. Frogs can and do learn by experience, but the extent to which they learn is very limited. They have been trained to find their way through a simple maze, and they are commonly trained to respond to signals that announce feeding time. But that is about as far as their learning goes.

The Endocrine System. As in other animals, coordination by the nervous system is supported by the action of the endocrine system. Experimental work on frogs and other amphibians shows that much the same hormones perform much the same functions in them as in higher vertebrates. This is highly significant in the light of evolutionary theory. It can hardly be a mere coincidence that excreted

Fig. 414. Circulatory system of frog.



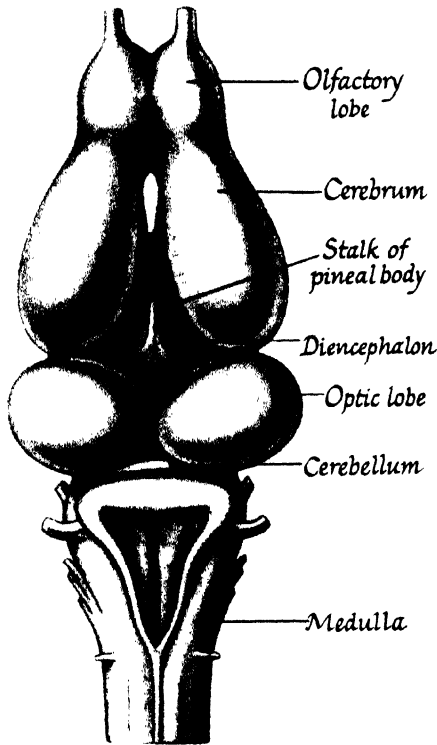


Fig. 415. The brain of the frog.

hormones from a pregnant mammalian female will cause ovulation when injected into female frogs, a now favored pregnancy test.

Reproduction. The bullfrog shows little specialization in reproductive structures above that of the average fish, though in different species many odd specializations are found.

In adaptation to land life, it may be said that the bullfrog is a long jump ahead of the

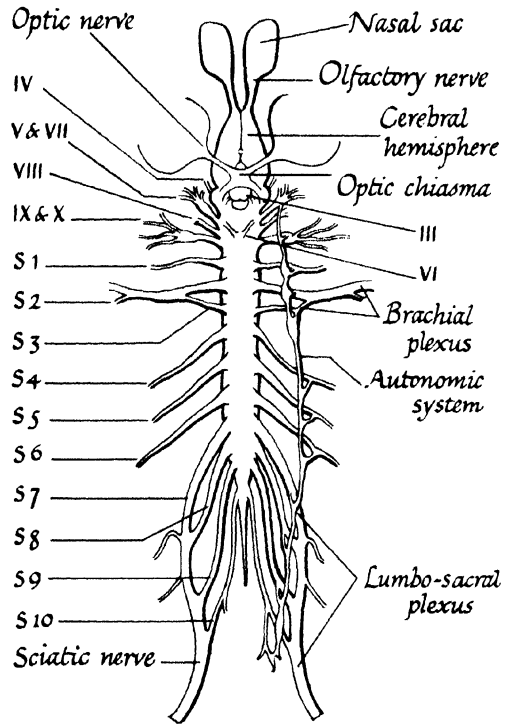


Fig. 416. Ventral view of nervous system of frog. (After Mavor.)

fishes — as indeed are the amphibians generally. In both fishes and amphibians, however, the main outlines of the vertebrate pattern are clearly shown — and such developments as the bony skeleton, the improved excretory structures, the swim-bladder and later the lung, fins and legs, and increasing coordination are essential steps toward the higher vertebrates, the reptiles, birds, and mammals.

The Great Transition: Reptiles and Birds

While the amphibians made great strides toward life on land, most of them are still denied the full freedom of the earth above the waters by the fact that they must lay their eggs in water, and that their free-swimming larvae develop there. But even as the amphibians reached about midway in the course of their own development, signs were beginning to appear of the next great stage in animal evolution, the movement toward total life on land, from birth to death.

THE REPTILES

The first reptile-like amphibians, aptly called "stem-reptiles," are well represented by *Seymouria*

Fig. 417. *Seymouria*, a link form between amphibians and reptiles (reconstructed).



mouria (Fig. 417). The very fact that this creature is sometimes thought of as an amphibian and sometimes as a reptile stresses its position almost midway between the two groups. Many of its skeletal characteristics are distinctly amphibian, whereas others are characteristically reptilian, and not shared by modern amphibians.

Seymouria flourished during the Permian Period, some 225 million years ago, but its species may date back well into the Carboniferous. It and its kind mark an extremely important stage in the evolution of life, for from the stem-reptiles arose all the higher vertebrates of today — the higher reptiles, the birds, and the mammals. Two rather late branches from this stem were (1) the turtles and tortoises — the most peculiarly specialized of all the reptiles — and (2) the scaly reptiles, the lizards and snakes. Earlier in the Permian Period, arose the archosaurs or "ruling reptiles," a group which later included the dinosaurs, among which were the largest creatures who ever trod the earth. Today, the only surviving branch of this once mighty group is the order *Crocodylia*, whose members are still well distributed throughout the tropical world.

In spite of the fact that their ancestors were the first real land animals, modern reptiles are a struggling remnant of a once dominant class. Of the sixteen or more orders of reptiles that flourished, but four remain, and one of these is all but extinct. Those that have survived are, as species, well but narrowly adapted, as attested by the limitation of their numbers and the wide differences between the orders. Reptiles are typically tropical animals, and those that live in colder climates are small and un-



Fig. 418. The tuatara of New Zealand (*Sphenodon punctatum*). The only living species of the order Rhynchocephalia.

obtrusive — for like the amphibians, they are cold-blooded and must seek safe hiding places in which to pass the winter, inert and helpless. Warm-bloodedness, the peculiar mechanism for the control of body heat which makes it possible for an animal to keep on functioning actively even during severe winters, did not appear until the arrival of birds and mammals. Thus while the reptiles broke the link that bound the amphibians to the water, they are still severely handicapped in the ability to range freely over the earth.

Reptiles are so divergent in form and outward pattern that it is difficult to give a general description of them. The reptilian body is generally divided into three more or less distinct regions, head, trunk, and tail. Except for snakes and some lizards, reptiles have four limbs. Most of them have dry skins with scales or scale-like structures and are thus easily distinguished from the moist-skinned amphibians. Except in the snakes, the eyes have movable lids. Reptiles show numerous increases in efficiency over amphibians in skeletal, nervous, circulatory, and excretory systems. Reproduction is adapted to life on land by the fact that fertilization is always internal — except in the most primitive member of the whole group —

and by certain very important developments in the reptilian egg, so that the larval stage is passed through in the egg, before hatching. Thus the reptiles at last are free of the water.

Sphenodon

The most primitive of modern reptiles is *Sphenodon punctatum*, commonly known as the tuatara. The only surviving member of a once flourishing order, this creature is now confined to a few outlying and isolated islands of New Zealand (Fig. 418), and is probably on the road to extinction. The tuatara is a nocturnal burrowing animal about two feet long. It retains several primitive reptilian features of great interest. One of these is the pineal eye, buried under the skin on top of the head, and presumably once functional in extinct primitive forms. Another is that certain features of the skeleton show that the animal is quite closely related to the original or stem reptiles, on the one hand, and also to the lizards, turtles, and crocodiles, on the other. It has four appendages, each with five fingers, and the notochord is incompletely replaced by the vertebrae.

Crocodiles and Their Relatives

A much larger and more flourishing group, the crocodiles and their relatives are now the

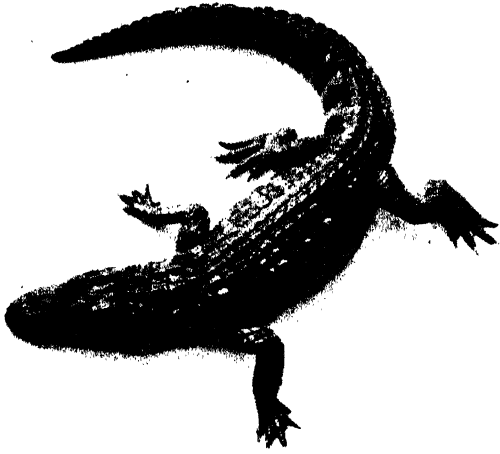


Fig. 419. The American alligator, a representative of the Crocodilia.

only surviving order of the once dominant archosaurs. While they are the largest living reptiles — some of them grow up to thirty feet in length — they are puny indeed compared to some of their ancestors (Fig. 419). Living mainly in the great rivers, especially in the tropics, some of the chief members of the group are the American alligator, the crocodile of the Mississippi and of the Nile, the caiman of the Amazon, and the gavials of the Ganges in India. These creatures are important to man mainly for two reasons. Some of them are extremely dangerous to human life, and the skins of some of the larger ones are so highly prized that numerous alligator farms have been established to breed the creatures for their hides.

The Crocodilia also show unique anatomical features. Their scales do not overlap, but are in the form of plates set upon dermal ossicles

and form a very effective armor against anything less powerful than a modern rifle. Alone among the reptiles they have a nearly complete muscular diaphragm which separates the lung cavity from the abdominal cavity, an organ otherwise found only in mammals. Equally interesting, the ventricle of the heart is divided into two complete chambers connected only by a small opening, so approaching the complete double circulatory system of birds and mammals. Moreover, like those of the mammals but not commonly those of reptiles, their teeth are set in sockets; but, like those of other reptiles, they are replaced when shed. The order has decreased rapidly in numbers, and in many areas faces extinction.

Turtles and Tortoises

Quite a different sort of armor from that of the crocodiles and alligators evolved in another reptile group, the *Testudinata*, the turtles and tortoises, which in this respect are the most oddly specialized of all reptiles (Fig. 420). The highly specialized exoskeleton of these creatures is intimately connected with the typical vertebrate endoskeleton and is thus of particular interest because of its origin as well as its structure. The box of the shell developed from enlarged and widened vertebral processes, ribs, clavicles, and supplementary dermal bones. All these fuse to make a solid mass of bone consisting of an upper shell, the *carapace*, and a lower one, the *plastron*. The outer surface is further covered with horny scales. Since the trunk vertebrae have been entirely immobilized, the muscles of that region, as well as of

Fig. 420. Modern turtles. The snapping turtle (left) and the North American soft-shelled turtle.





Fig. 421. Types of lizards. Above, left: The flying dragon of the Malay peninsula, *Draco volans*. Right: The Gila monster, *Heloderma suspectum*, the only poisonous lizard. Below: The Komodo dragon, *Varanus komodensis*, largest lizard now living, attains a length of ten feet.

the abdomen, have atrophied completely, while the limb musculature is correspondingly overdeveloped. Because of the rigidity of the body, the mechanism of breathing is also peculiar. Air is partially swallowed, partially pumped in and out by movements of the neck and limbs.

Land turtles, to which the name tortoise is generally applied, are mostly herbivorous, while turtles living in the water are largely carnivorous. Reproduction is by means of leathery eggs laid on land, buried in sand, and left to hatch without parental care.

Lizards and Snakes

The fourth surviving group of reptiles includes the lizards and snakes and is known as the order *Squamata* (Lat. *squamatus* = scaly), so named because a scaly skin, which is shed periodically, is the chief distinguishing mark of the group. Most lizards are quadruped, and as a group they are the most "typical" of the modern reptiles. That is, they are on the whole least specialized, except for peculiar individual cases. Other lizards range from a few inches in length (Fig. 421) to such giants as the Komodo dragon, which reaches a length of as much as ten feet.

Among specialized lizards, the true chameleons are the most aberrant (Fig. 422), so that sometimes they are even considered to be a

Fig. 422. The Sudan chameleon, *Chamaeleon basiliscus*. Prehensile tail, grasping feet, laterally compressed body, protrusible and laterally compressed tongue are evident.



separate order. They are famed for their striking changes in color, although certain other lizards quite match them in this ability, the so-called Louisiana "chameleon," for example. They are more striking, though less well known, for their specializations for arboreal life. The body is laterally compressed; the tail is prehensile; the foot is claw-like, composed of three fused toes opposing the other two, which are similarly fused. The protrusible tongue is sticky, and can be hurled almost a body-length for the capture of insects. The eyes are independently movable, and apparently their vision is keen. Reproduction is viviparous. Most of these characteristics, it will be observed, show some degree of adaptation to life in trees.

Another striking specialization is that of the flying dragon, *Draco volans*, of the East Indies, which has a membranous lateral fold of skin supported by oddly extended ribs. With this structure spread like an umbrella, it can glide appreciable distances from tree to tree. *Amblyrhynchus cristatus*, the crested lizard of the Galapagos, is the only living marine lizard and the only one which feeds entirely on aquatic plants. But it is by no means the only vegetarian among lizards, for others live on buds and shoots. Most lizards, however, are carnivorous or insectivorous.

Only one of all the lizards is poisonous, the Gila monster, a sluggish, clumsy, and fearless creature. Its bite is deadly to small animals, but rarely to man. A poisonous saliva, secreted around the base of grooved teeth, is worked into the wound by deliberate chewing movements.

Snakes (Fig. 423), are limbless, except for rudimentary hind limbs in some pythons and boas, and they have lidless eyes, which give them their traditional glassy stare. A soft forked tongue, extended through a notch on the upper lip, serves as a delicate organ of touch. Locomotion is by winding movements, much like those of swimming, as well as by the centipede-like action of the numerous ribs, aided by the slightly protruding rear edges of broad, flat scales on the ventral surface. The specialization of the feeding mechanism is extraordinary.

Snakes swallow their prey whole, though some first crush it by coiling around it. The jaw can be enormously distended, laterally as well as dorso-ventrally, because the lower jaw articulates only indirectly with the skull by means of two elongated bones. At the snout, the two halves of the lower jawbones are joined only by elastic tissue and thus can be spread apart. With such a mechanism, snakes can swallow objects several times their own diameter. Aided by the incurved teeth, opposite sides of the jaw are hitched forward alternately, until the mouth is drawn over the prey.

The poison mechanism of poisonous snakes is intricate and beautifully precise. In some snakes, the fang is still merely a grooved tooth, similar to but more perfectly adapted than that of the Gila monster. In others, the groove has become a closed channel with a small opening at the base and another near its tip (Fig. 424). It is thus in truth a hypodermic needle. The poison glands, above the angle of the jaw, empty the venom at the base of the fang, which is wrapped round by a funnel-like flap of tissue. When the snake lifts its head and opens its mouth to strike, the lever action of a series of bones automatically elevates the fangs from their normal infolded position until they project from the roof of the mouth at right angles. The snake strikes by lunging, usually to a distance not greater than two-thirds of its length, and thus injecting venom into the wound. The poisonous snakes in this country are the rattlesnakes (*Crotalus*), the water moccasin or cottonmouth (*Agkistrodon piscivorus*), the copperhead (*Agkistrodon mokasen*), and the beautifully colored little coral snake (*Elaps fulvius* and *E. euryxanthus*).

Reptilian Embryology: Membranes

One of the things which made land life possible for the reptiles was a series of embryological advances which set them off distinctly from the amphibians and freed them from their dependence on the water as an environment. The reptiles have no aquatic larvae and no metamorphosis. They lay large eggs packed with stores of food and surrounded by three

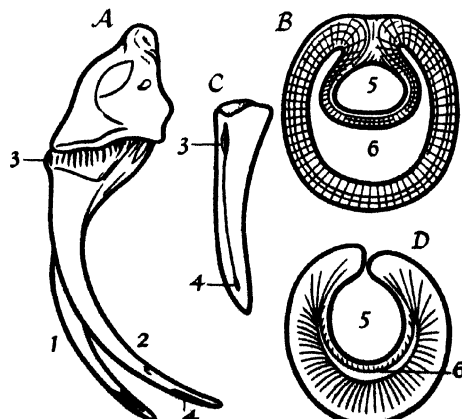


Fig. 423. The hognose snake or spreading adder, *Heterodon platyrhinos*. Female and eggs.

embryonic membranes. The young can consequently develop far more completely before they hatch, and can begin their lives as breathers of air. These same embryonic membranes are also found in birds and mammals, and thus definitely set apart these three classes of vertebrates from the fishes and amphibians. Reptiles and birds show great similarity in their eggs and embryonic development, while mammals, though preserving the same membranes, show considerable modification with the advent of the intrauterine development of the embryo within the mother.

The first and outermost of the three embryonic membranes is the *chorion* (Fig. 425). The embryo then produces a second membrane, the

Fig. 424. A. Upper jaw of the Fer-de-lance, *Lachesis lanceolata*, showing one active fang (1), and one in the process of being discarded (2). B. Cross-section of fang of *Lachesis*. C. Fang of cobra. D. Cross-section of cobra fang: (3) incurved and (4) excurrent openings for venom; (5) venom channel; (6) pulp cavity of tooth. (A after Kathariner, B after Leydig, C and D after Boas.)



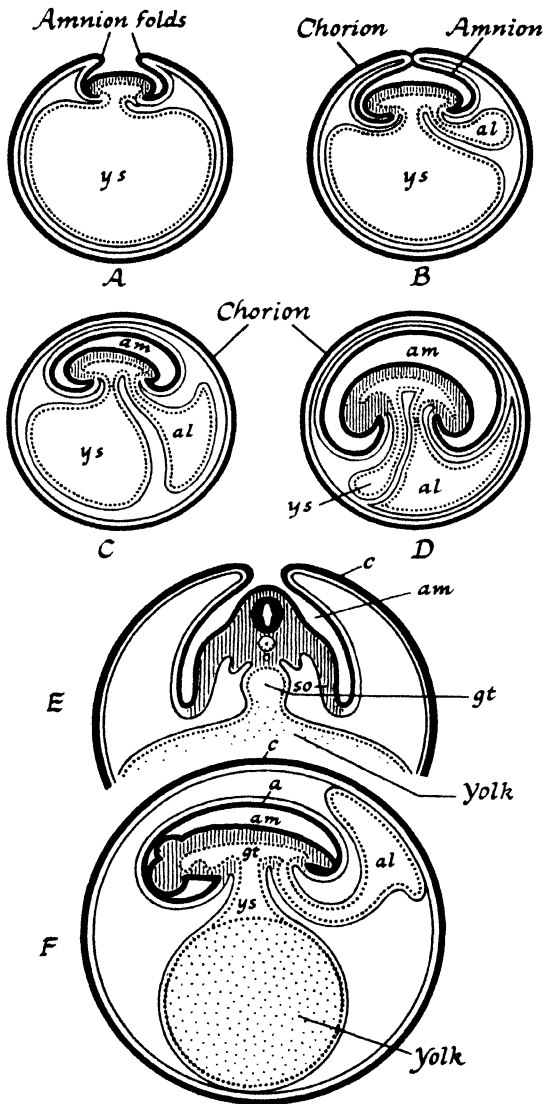


Fig. 425. Diagram illustrating the development of fetal membranes in the chick. (After McMurich and Kingsley.) In A–D, ectoderm, mesoderm, and endoderm are represented by heavy, light or shaded, and dotted lines respectively. *a*, amnion; *al*, allantois; *am*, amniotic cavity; *gt*, gut; *so*, somatic peritoneum; *ys*, yolk stalk and sac.

amnion, in the shape of a sac growing from the two sides and completely surrounding the dorsal half of the embryo. It becomes filled with a fluid which protects the growing organism from mechanical shock, from severe changes in temperature, and from drying out. Thus in a sense this membrane provides an aquatic en-

vironment for the embryo, in essence very much like the watery environment of the eggs of fishes and amphibians. The amnion is of extreme importance in enabling the reptiles, birds, and mammals to dwell on land, and these groups are known as *amniotes* in distinction from the fishes and amphibians (*anamniotes*) which do not possess the membrane. The last of the embryonic membranes, in time of development, greatly assists in respiration and excretion. This is the *allantois*, formed by an outgrowth of the posterior part of the intestine. Through it carbon dioxide is given off and oxygen is taken in — the outer shell itself being permeable to these gases — and in later stages it serves as a place where waste products may be deposited and accumulate without harm to the growing embryo. It is difficult to imagine the embryonic development of reptiles without these membranes.

Other Developments

The skin of reptiles, like that of all higher classes of vertebrates, consists of stratified, plate-like epithelial cells. Scales are horny epidermal layers formed upon the papillae of the dermis. In lizards and snakes, the outer layer of skin is periodically shed, sometimes in one piece like a stocking removed from a leg. In crocodiles the scale papillae are ossified to produce the dermal ossicles. All this is a long step from the simpler glandular skin of the amphibians.

Teeth are generally conical and are shed periodically. Extinct mammal-like reptiles exhibit various stages of tooth development, from the unlimited replacement system of reptiles to the type of mammalian pattern already evident in the cynodonts, in whom all but the molar teeth are replaced only once in the lifetime, while the molars are permanent.

The reptilian kidney is a metanephros, as contrasted with the mesonephros of the Amphibia. The circulatory system shows those advances which might be expected along with the increased activity and metabolism required by life on land. Devices that partially separate

oxygenated from unoxygenated blood in the heart range from simple ones much like that in the heart of a frog, to the complete separation of the ventricles into two chambers, as in the Crocodylia. The basic scheme (Fig. 382) is that of three arteries which distribute unoxygenated, mixed, and oxygenated blood to the lungs, body, and head, somewhat as in the bullfrog. This form of circulation is about midway in efficiency between that of a typical amphibian and that of birds and mammals.

The nervous system shows several advances over that of the amphibians. The cerebral cortex especially shows more extensive development, although it is still very limited compared to that of the mammals.

VERTEBRATES IN THE AIR: THE BIRDS

All vertebrate classes have evolved forms which are capable of flight, but the entire anatomy and physiology of birds (*Aves*) is built around this, their outstanding characteristic, and relatively few have lost this ability. Closely associated with flight in birds is their unique and characteristic body covering, feathers. In the special adaptations found in their other structures also, flight has apparently been the guiding selective factor. Thus birds have a hollow-boned skeleton, most of them have a deep-keeled sternum or breastbone, they all have bipedal locomotion on the ground, warm-bloodedness (associated with an extremely high metabolic rate), they lay eggs instead of carrying the unborn young within their bodies as mammals do, and they have a relatively well-developed brain. All these characteristics are prerequisite to really successful flight.

Aside from these adaptations to flight, birds share many structural features with reptiles, and especially with the once mighty archosaurs or "ruling" reptiles, of which they may be said to be glorified descendants. This is evident both from comparative anatomy and from fossil remains (Fig. 71). The fossil record is very spotty, for delicate bird bones are not often preserved. Nevertheless, the broad pattern of bird evolution is fairly plain. The primitive Jurassic *Archaeornis* (Fig. 426) and its

close relative *Archaeopteryx* are probably as perfect "missing links" as any that could be imagined. In each, the slender snout still bears teeth. The anterior appendages have three well-developed fingers. There is no keel, indicating feeble flight muscles and hence poor flight. The feet are typical bird feet, but the tail is like that of a lizard. We know that the animal was clothed in feathers, for the imprints of feathers are clearly preserved in the lithographic limestone in which the creature was preserved. In view of its insulating body covering, it is almost certain that the animal was warm-blooded and was presumably active, with a high metabolic rate. It appears most likely that this primitive bird was a tree-dweller, jumping from branch to branch and extending its leaps into a glide by means of its wing surface. That this would be of selective

Fig. 426. Restoration of primitive Jurassic bird, *Archaeornis*.



value is obvious, and thus flight probably began and was perfected. Judging from the lesson taught us by modern flightless birds, it appears likely that a kind and gentle environment would never have produced such birds as we know today.

The eminent success of the basic bird-pattern is evident in its enormous diversification within closely held limitations. Even so, this pattern has been adapted to practically every form of environment and mode of life. Ostriches outrun horses. No other vertebrates can match the flight of such birds as swallows. Penguins compete with fishes in their own element. Yet even these extreme types adhere closely to the basic pattern. That this holds true for flying birds is not surprising; that it is also true for flightless birds is perhaps less obvious.

There are nearly 10,000 species of birds (class *Aves*). These have been divided into two subclasses, the first including only extinct birds, the second, modern birds; and the latter in turn are of two kinds, since some are flightless. The flightless group (Fig. 427), the *Ratitae* (Lat. *ratit* = raft), contains but four orders; the winged group, the *Carinatae* (Lat. *carina* = keel), includes twenty-one (Fig. 428).

General Structure

The general architecture of birds is remarkably uniform, despite differences in size and way of life. The body is approximately drop-shaped, that is, streamlined for swift movement through the air. Because the body is rigid, as

it must be for flight, the neck is long and flexible in compensation. Except for their occasional use in swimming, wings have been strictly modified for flight, and their claws, except in a single species, the hoatzin, have been lost altogether. Even in birds where flight has been lost, the wings have not been adapted to other uses. Legs vary widely, according to mode of living, but their basic design is the same. The bird's foot is a highly evolved grasping and walking organ containing a minimum of living tissue. The remainder of the body is covered with feathers, highly modified derivatives of reptilian scales.

Feathers

The contribution of feathers to efficiency in flight cannot be overemphasized. Light, flexible, strong, and smooth, they provide an ideal flight surface on wings and body. Moreover, the feathers of a bird serve as insulation and make possible a high body temperature and thus the high rate of metabolism necessary for rapid and sustained flight. Feathers also allow great variation in color pattern, and in some species even for changes in color to suit the environmental needs of the season. Feathers lost through wear and tear are replaced after annual or semiannual molts.

No structure in any living organism shows more perfect adaptation to the function it performs than a feather. Consider the requirements to be fulfilled. Feathers must help to retain the body heat, for the bird is warm-

Fig. 427. Wingless birds, the ostrich and the kiwi.



blooded. They must be light and still withstand rough usage and rapid movement through the air. They must also be reasonably waterproof. In flight, they must produce a flexible but rigid and unbroken surface, yet one that can be folded up; and, if possible, they should be self-repairing if torn. Feathers do all this, and more, for flight is no mere flapping up and down of wings. Flight is a highly coordinated movement, more delicately performed than the feathering of oars by a skilled oarsman. Not only are the wings moved in a rowing action, but each feather automatically adjusts itself to present a full carrying surface on the downstroke and a minimum of resistance on the upstroke. To appreciate this fully, a closer examination of the structure of a feather is necessary.

Feathers in different parts of the body differ in shape, depending on their various special functions. For insulation the feathers should be loose, woolly structures that provide as much dead air space as possible. But for protection against rain and wind, a smooth continuous surface is best. Therefore some are downy and maintain an air film around the body. Between them, and reaching to the surface, are others which are downy at the bottom but have a smooth continuous surface near the tip. These tips overlap like shingles on a roof, an effective arrangement for shedding water and reducing friction with the air. The flight feathers are somewhat different, and these present the finest engineering feat of all.

Viewed under a microscope, a feather is a sight to admire (Fig. 429). It looks as if it were actually composed of thousands of smaller feathers, with their vanes overlapping. The central shaft or quill of the feather is hollow for greatest strength with minimum weight. Angling from it in two opposed rows are similar but much smaller lateral shafts called barbules. Angling out from these again are minute structures somewhat like flattened hairs or long scales, ending in filamentous tips. Closer observation shows two kinds of these structures. Those along one side of a barbule are straight and quite smooth, but those on the opposite

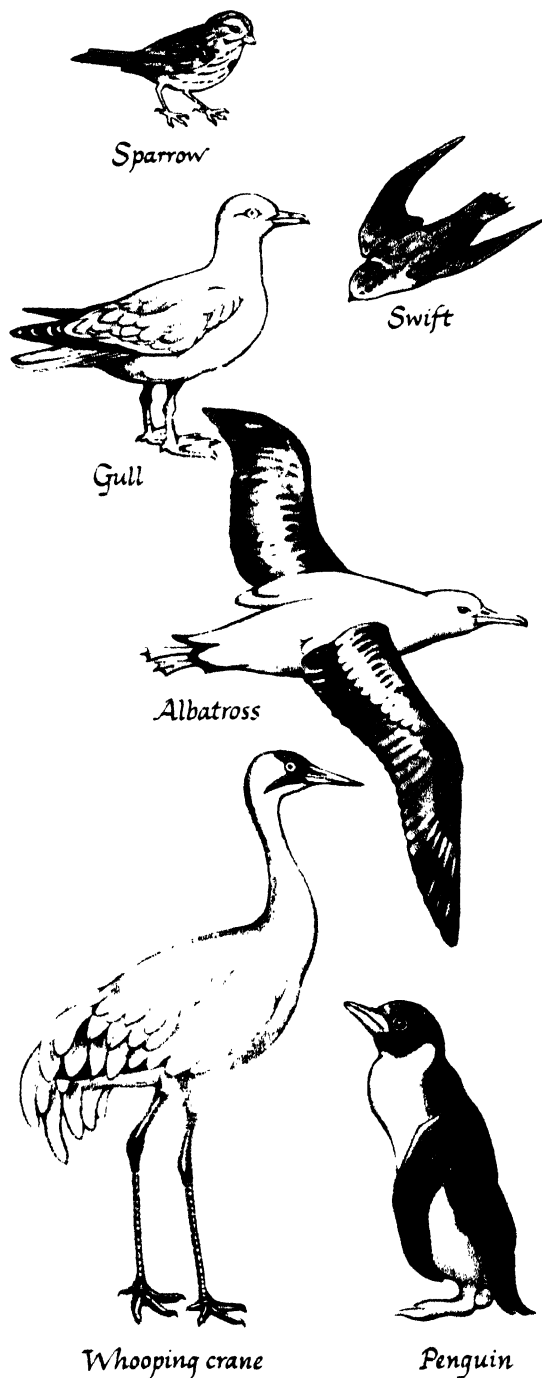


Fig. 428. Even the winged birds show considerable variety within the basic pattern.



Fig. 429. Details of feather structure. A. Flight feather. B, C, and D. Details of quill and vanes, showing barbules.

side have sharp spines and incurved hooks attached to the filament. Normally, the hooked filaments of one barbule overlap the straight ones of the adjoining barbule, thus firmly anchoring one to the other. Stretch the surface of a flight feather, and after some elastic yielding, it "tears." Now stroke it between thumb and finger, and the tear mends itself perfectly. This is nature's first zipper, over a hundred million years old. What a bird does when it draws its feathers through its beak in preening is literally to "zip them up" again.

There are still further mechanical refinements to mention. The vane of the flight feather is wider on one side than on the other. This difference is important, for on the upstroke of the wing, air pressure on its surface pushes unequally on the two vanes of the feather, more on the wide side, because of its greater surface, than on the narrow one. This makes the feather swivel on its shaft, and the entire wing surface opens up much like a Venetian blind, permitting the air to pass through and so greatly reducing the resistance of the wing. On the downstroke there is a similar distribution of pressure, but now, instead of swiveling, the wide vane surface of one feather is pushed tightly against the underside of the adjacent one, so as to present an unbroken surface. When wear and tear damages even this self-healing and resilient surface, the feathers are shed, the bird molts, and new feathers take the place of the old.

Warm-Bloodedness

The land animals previously considered are severely limited in their activities by the fact that their body temperature is not evenly maintained by internal regulation, and consequently their range of activity is severely curtailed. Amphibians and reptiles, for instance, are so much at the mercy of variable climate that in cold weather their metabolic activities are slowed almost to cessation and they are forced to hibernate. Such animals are called cold-blooded. Birds and mammals, however, alone among living things, are warm-blooded. That is, their body temperatures are regulated internally and remain fairly constant regardless of climatic changes. The result is that their metabolic rate is high. That of birds exceeds that of almost any other animal, their body temperature ranging from 105° F. to 108° F.

While the feathers of birds and the hairy covering of mammals provide insulation which helps keep body heat in, increased temperature is actually both a result and a cause of increased metabolism and is thought to be under the control of a specific region of the brain, the diencephalon. It is believed that messages from this area create a balance between heat production and heat loss. Heat is produced by increased oxidation, and its loss may be partly controlled by the dilation of blood vessels, and consequent radiation of heat, near the surface of the body, or, conversely, by contraction.

Though warm-bloodedness brings with it certain disadvantages — the life of the bird is a constant search for food — its advantages far exceed the disadvantages. The enormous expenditure of energy of which birds are capable is made possible only by warm-bloodedness, which gives them an advantage over cold-blooded competitors in speed and action as well as in sustained activity. Perhaps even more important is the increased range of activity made possible by this characteristic, including the ability to remain active in variable climates for more than a limited portion of the year, and the consequent increase in control over the environment. The sight of a one-ounce chickadee blithely facing a sub-zero world epitomizes the advantages which a constant body temperature confers on its possessor.

Anatomical Features

The skeleton of the bird, while typically vertebrate, is also highly specialized for flight. The tubular bones are very strong; weight for weight, far stronger than solid ones would be, since a tube is stronger than a solid rod of the same weight and length. The rigid body firmly supports the flight muscles, and the flexible neck provides needed mobility. The muscular system is remarkable only for its enormous development of the flight muscles, which are anchored to the deep keel or breastbone.

The digestive system is highly efficient and capable of prodigious performances. Probably no other living creatures, with the possible exception of shrews, consume as much food in proportion to their weight as birds. This is to be expected in view of their high temperature, relatively small size, and enormous activity. Insectivorous birds may consume up to two or three times their body-weight in food per day. Larger birds, and especially meat-eaters, consume considerably less. An eagle can endure a starvation period of four to five weeks; a small insect-eater, only two to three days; and a grain-eater, such as a canary, not even two days.

Since birds are relatively defenseless and rely upon speed and alertness for survival,

their digestive system is constructed for rapid ingestion. For this purpose there is frequently a *crop*, that is, a widened section of the esophagus which serves for the temporary storage and softening of rapidly swallowed food. In some birds, this region may be highly glandular, thus aiding in digestion. In others, such as pigeons, it produces a milk-like secretion which is fed to the young. The stomach proper is a muscular organ, varying widely in different species. In birds that eat hard seeds, the stomach or gizzard becomes a crushing-mill with the aid of swallowed pebbles and sand grains, while in meat-eaters its action is mainly chemical. The intestinal tract is relatively short. Like other vertebrates, each bird has a bile duct that leads from the liver into the duodenum, and a pancreatic duct from the pancreas to the duodenum. A short rectum terminates the intestine and ends in the cloaca along with the urogenital tract. There is a metanephros, which discharges directly into the cloaca without benefit of a bladder.

The circulatory system is a modification of the reptilian design. The two aortic arches of the Crocodilia are reduced to a single one in birds, just as in mammals; but in birds it is the right one that survives, whereas in mammals it is the left. The heart, as in mammals, has four chambers, and the system is completely double.

Respiration is efficient, and indeed must be to sustain the high metabolic activity. Air sacs greatly increase the efficiency of lung ventilation, and since there is no diaphragm, air is pumped in and out by the action of the abdomen and of the ribs. Vocal equipment is common, and in some birds highly developed — witness the beautiful songs of the thrush, the nightingale, and the lark, and the ability to mimic human speech of the parrot and black-bird.

Coordination is highly developed, in keeping with the needs of creatures who engage in such swift, split-second aerial acrobatics. The cerebrum is small compared to that of mammals, but the coordinating cerebellum is enormous and the optic lobes are well developed. Of all

the vertebrates, only birds have striated muscles within the eye for the accommodation (focusing) of this organ. In keeping with the all-important role of vision in certain birds, such as hawks and owls, the eyes are often relatively enormous. Thus in the sparrowhawk the eyes occupy almost two-thirds the entire volume of the head. In birds, the cochlea or hearing organ of the inner ear is flask-shaped in contrast to the tightly wound snail-like structure present in mammals. The three bones of the mammalian middle ear are represented by only one. Despite this apparently greater simplicity, the ability of some birds to learn human speech and to sing complex songs indicates the high efficiency of their hearing mechanism as well as their vocal capacity. Taste and smell are but poorly developed in most birds.

Reproduction

Courtship and mating reflect the high metabolic level of birds, since these activities are tempestuous and often marked by intricate and highly interesting procedures. Fertilization is internal, although the organs of copulation are quite small, probably as an adaptation to the need for reducing weight. The young birds develop from highly specialized and relatively large hard-shelled eggs which are laid promptly after completion, a necessary adaptation in flying creatures. Interestingly enough, this occurs even in birds that no longer fly. After an incubation period of several weeks — usually varying with the size of the egg — the

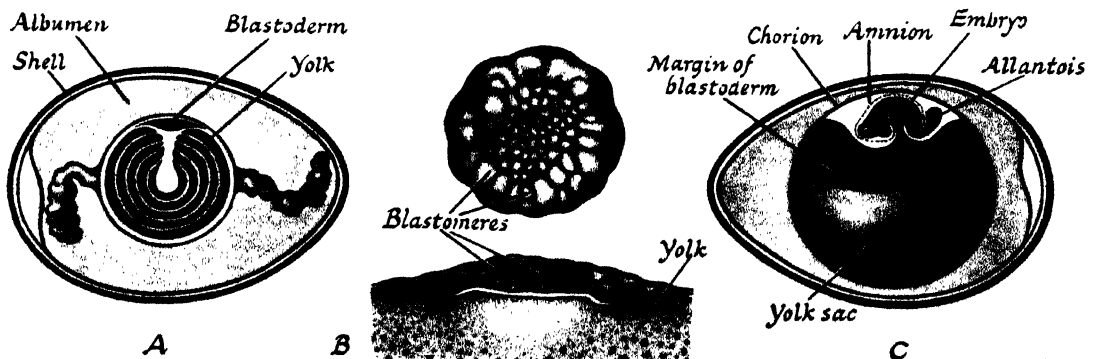
young are hatched. Their condition at this time varies from complete nakedness and blind helplessness to almost complete independence and self-sufficiency. Small flying birds lay relatively small eggs and their young are blind and naked at birth — these are of the *altricial* type (*L. altrix* = nurse). Larger ground birds lay larger eggs which hatch into downy young. These are soon relatively self-sufficient, and are said to be *precocial*, like the baby chick. Similar differences exist in mammals, and we are reminded of the difference between a newborn kitten, which is born naked, blind, and helpless, and a colt, which can stand on its legs almost immediately after birth.

Embryology of the Chick

We have already seen that reptiles, birds, and mammals have a distinct advantage over the lower vertebrates because of the embryonic membranes which make it possible for the young to develop so completely before birth and which go hand in hand with the disappearance of the larval stage. The egg of a bird is quite similar to that of a reptile and in a broader sense to that of the mammal also.

The Unincubated Egg. In a representative bird's egg, e.g., that of a chicken, the egg proper is the "yolk" (Fig. 430). This is a single cell enormously bloated by the inclusion of stored food. At the time of ovulation, a delicate but relatively tough cell wall, the vitelline membrane, covers the yolk. The egg is fertilized in the oviduct, and now becomes surrounded by the egg-white, or *albumen*, and by a shell

Fig. 430. The egg and early embryonic development of birds. *A.* Diagrammatic longitudinal section of hen's egg before incubation. *B.* Early blastula stage in pigeon (after Blount). Above: Surface view of blastoderm. Below: Vertical section of blastoderm. *C.* Relation of a five-day-old chick embryo to the egg.



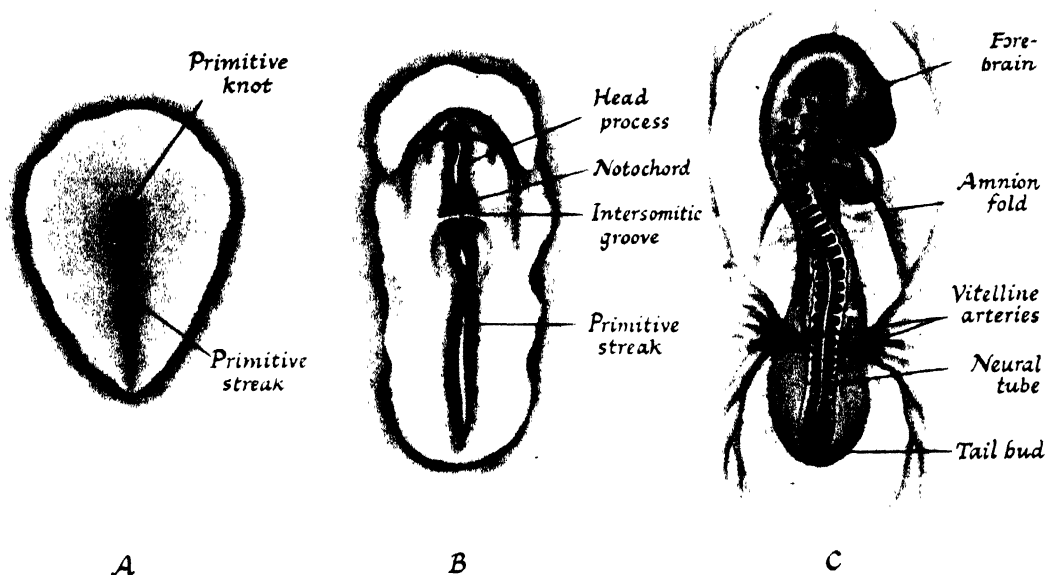


Fig. 431. Stages in the embryo of the chick. *A.* Surface view of blastoderm at 16 hours' incubation, the stage of the primitive streak. *B.* Dorsal view of embryo at 21 hours' incubation, as segmentation begins. First intersomitic groove is visible. *C.* Embryo at 50 hours' incubation (27 segments). Note amnion fold, and branching vitelline arteries and veins which bring food from yolk to embryo.

membrane, and is finally covered by the porous but hard shell itself. The first steps in development, through gastrulation, are completed at the time of laying, and the gastrula forms a visible white disk on the yolk, the *blastoderm*, several cell layers thick.¹

Cleavage. Because of the very large amount of inert yolk in the egg and the relatively small amount of living protoplasm, which occupies but a small area on the surface of the yolk mass, cleavage is only partial and is called discoidal, for the first cleavage stages produce a disk of cells (blastomeres) on one pole of the yolk mass (Fig. 430). The simple type of gastrulation seen in *Amphioxus* is modified in the Amphibia because of the large yolk-filled cells at the vegetal pole. In birds it is still further modified, and the endoderm is formed mainly by a splitting away of a second layer from the surface layer of cells. As the blastoderm increases in area by further growth, the dorsal lip of the blastopore — referred to as the primitive knot

— assumes the form of a long thickened streak, the primitive streak, and it is from this that mesoderm arises (Fig. 431). A cord of cells extends forward from the primitive knot — this is called the head process. Within it, the notochord develops, and above this is a thickened groove, the *neural fold*, later to become the nerve cord. Thus the central features of the embryo are established.

During this process, the blastoderm continues to grow as an ever-widening cap on top of the yolk mass. Blood vessels and blood have formed, and so has a simple ventral tubular heart, though this is not visible in the illustration. The embryo is growing now at the expense of the hydrolyzed yolk material being transmitted from the outlying, extra-embryonic tissue of the blastodermal disk by the newly formed blood-vascular system.

Formation of Embryonic Membranes. At the end of the second day of incubation, the chick has reached a stage of development at which it has twenty-seven segments. Now a crescent-shaped fold rises from the extra-embryonic ectoderm surrounding the embryo proper, and the embryo sinks down into it until, like con-

¹ Despite this, fresh-laid fertilized eggs may be kept in cool storage for weeks before starting their incubation. Eggs produced for the market are generally infertile, since only hens are kept in the laying-house.

verging waves breaking over its head, the folds join and completely cover the embryo with a double set of membranes. The outer ectodermal fold, with a mesodermal lining, is the chorion — of little significance in birds, but very important in placental formation in mammals. The inner layer of the fold — also with a mesodermal lining — is the amnion, within which the embryo floats in the amniotic fluid. Now another fold or pocket grows out of the posterior gut cavity of the embryo. This is the allantois, or embryonic bladder, which is the chief respiratory, as well as excretory, organ of the embryo. Once the main outline of chick anatomy becomes established, further development of the embryo consists of an elaboration of organs already begun.

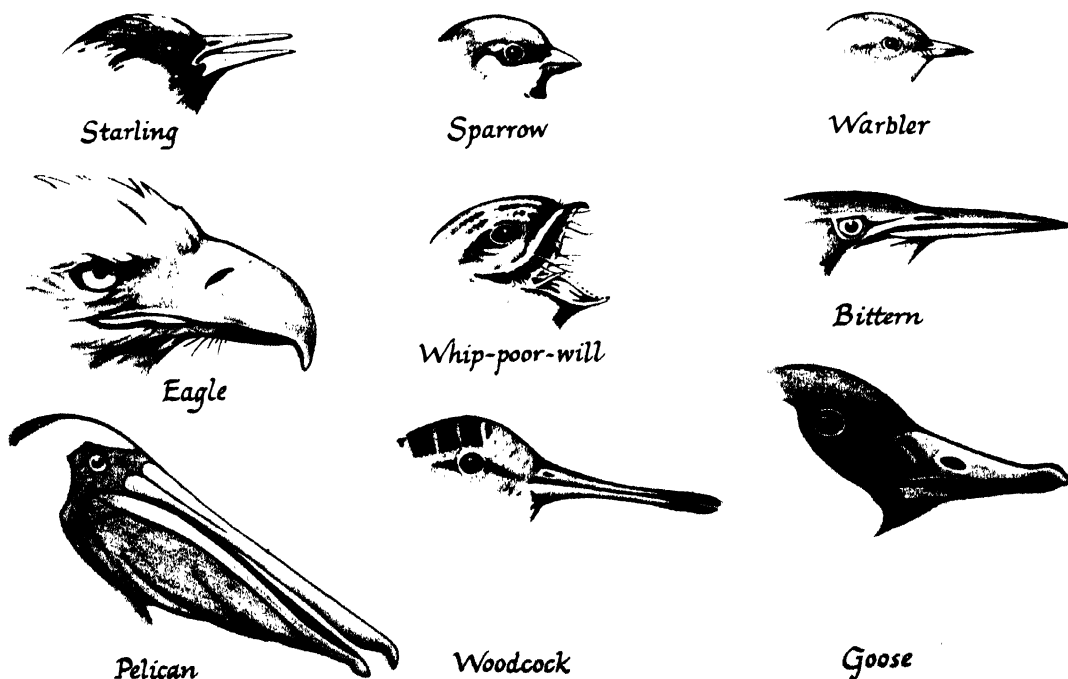
Adaptive Divergence

There is little variation in the basic design of birds, and in number and variety their diverse adaptations fail to approach those of most other vertebrate classes. Still, the variations are numerous enough. The flightless birds are perhaps the most striking variant from the norm. These are scattered over the southern

continents, the most prominent among them being the rheas of South America, the emus and cassowaries of Australia, the kiwi of New Zealand, and the ostriches of Africa. Until almost recent times, there was another, the moa, a twelve-foot monster of New Zealand, apparently exterminated by the Maori natives.

It is perhaps significant that most of these birds live in territories where there are no large predatory animals, or, like the ostrich, on wide, open plains where escape is easy for a fleet-footed animal. This fact, and the existence of flightless birds of other orders on small islands, suggests that flight is primarily a means to secure safety. Where flight becomes unnecessary, it appears to be a luxury and hence a burden — perhaps because of its excessive cost in fuel. Like any other attribute, it is lost when its selective value disappears, and with birds this happens when there are no dangerous enemies. Thus a flightless pigeon, the dodo (*Didus ineptus*), lived safely on the islands off Madagascar apparently until the year 1681. It was a fat, grotesquely clumsy bird, larger than a turkey and delicious to eat. But for man, its flightless existence on the islands

Fig. 432. Adaptive variations in the beaks of various birds. *A.* Starling. *B.* Sparrow. *C.* Warbler. *D.* Eagle. *E.* Whippoorwill. *F.* Bittern. *G.* Pelican. *H.* Woodcock. *I.* Goose.



would have been peaceful and secure, and flight completely useless. It was killed off by European sailors. Penguins, which appear to have had a similarly untroubled life, have also lost the ability to fly and so are marooned on remote islands and on the Antarctic ice shelf. Flight thus appears to serve mainly for escape, or, in birds of prey, for pursuing food. Its success cannot be doubted, but as a means of obtaining dominance over the environment, it appears to be of doubtful value. Birds can never hope to dispute territory with advanced mammals of similar size. Their specialty, in every sense, is flight.

Birds also show a variety of modifications in beaks, tongues, and feet. In all modern birds horny beaks envelop the jaws and replace teeth. In most birds, the beak is a universal instrument, used for eating, grooming, exploration, defense, and attack. In many birds, however, the beak has evolved into a highly specialized tool for the performance of some one special operation. It may then show a merely superficial adaptation in shape, or it may involve considerable modification of skull and tongue as well.

Beaks. The beak of the starling is typical of the general instrument (Fig. 432). The seed-hulling beak of the sparrow is much the same, though it shows some adaptation. Less generally useful, perhaps, is the delicate stiletto of a typical insectivore, such as the warbler. The beak of the eagle is a fleshing hook. The small beak of the whippoorwill hides a gaping mouth fringed with long hairs, making it a suitable trap for insects, which this bird catches on the wing. The beak of the bittern is a deadly spear for frog or fish. In the pelican the fish-spear is transformed into a roomy satchel for transporting the catch. More involved is the beak mechanism of the woodcock. By a system of delicate bone levers and muscles, the tip of its beak is movable and can be opened without opening the angle of the jaw. Thus it can be inserted into the ground as a probe, and when the sensitive tip detects a grub or worm, the end alone can be opened to grasp it. Highly specialized, too, are the beaks of goose and

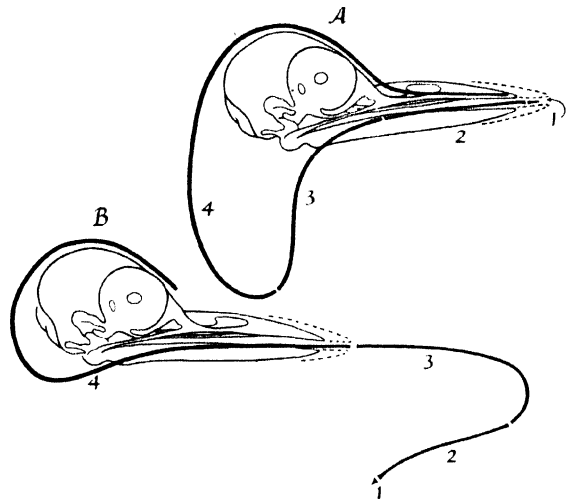


Fig. 433. The tongue mechanism of the woodpecker (*Picus viridis*), retracted, and extended in harpooning position. Numbers show positions of comparable portions.

duck, which are entirely covered with a sensitive membrane, making them organs of touch with which to probe and feel. The margin of the beak is finely frayed and provides a filtering screen. Water pumped in through the tip of the beak by the piston-like tongue is ejected laterally, so that even the finest particle of edible material can be screened out of the water sucked from the ooze and mud of a pond.

Tongues. Tongues, too, come in all sizes and shapes. Perhaps the most remarkable is that of the woodpecker (Fig. 433), which is enormously long and supported by small ossicles. The base of this tongue is bifurcated and extends into a loop in the neck, passes under the base of the skull, around over the top of it, and into the upper half of the beak. The tongue is four times as long as the beak and can be extended like a harpoon. Its tip, equipped with a thin sharp bone, has lateral barbs with which grubs can be speared even in their burrows within a tree. Well developed glands below the jaw secrete a sticky saliva which further increases the efficiency of this tongue.

Feet. The foot of the bird (Fig. 434) is in some ways more like a mechanical instrument than a living organ. It is light, relatively strong, and insensitive — a remarkable structure. Both the foot and the leg are covered

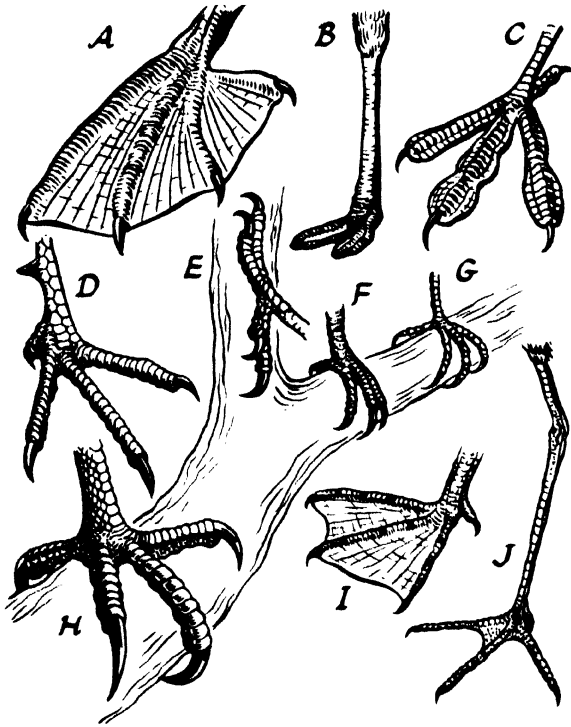


Fig. 434. Adaptive variations in the feet of birds. *A.* Totipalmate swimming foot of the cormorant. *B.* Running foot of ostrich. *C.* Foot of the coot or mudhen, lobate for soft mud. *D.* Walking and scratching foot of pheasant. *E.* Foot of flicker, for clinging to vertical surfaces. *F.* Perching foot of kingfisher, with partly fused toes. *G.* Perching foot of yellowthroat, a warbler. *H.* Clutching and piercing foot of hawk. *I.* Swimming foot of blue-winged teal duck. *J.* A wading foot of greater yellowlegs.

with horny scales, a truly reptilian heritage. In perching birds, the foot is an automatic locking device, so constructed that when the bird alights, its toes effortlessly close about the branch and remain so locked until the leg is again straightened. Most bird feet have four toes, three in front and one behind, but both foot and leg have been interestingly modified for many different functions (Fig. 434). Wading birds have long legs and long toes which

distribute their weight on spongy ground. Soft mud calls for a large surface, and in the coot such a surface has appeared in the form of a lobed foot. Many birds have webbed feet used in swimming. In the cormorant the web involves not only the anterior three toes, but the posterior one as well. One of the least specialized kinds of foot is that of a walking or running bird, such as the pheasant. Small birds, warblers, for example, have delicate feet that serve only as clamps. The toes of hawks are equipped with lethal daggers. The kingfisher uses its foot exclusively for perching on twigs, and two of its toes have begun to fuse into a single unit, as in the chameleon. In the flicker, the strain on the posterior toe while clinging to vertical surfaces, has been relieved, since one of the anterior toes has become turned to the rear. Most unusual is the ostrich's two-toed foot, strongly reminiscent of the reduction in number of toes that occurred in hoofed running mammals.

The variations in form, color, habits, and many other characteristics found in birds are virtually inexhaustible, yet they all come within the frame of the typical and fairly limited body pattern of the class. There is not much to be said about birds as contributors toward vertebrate evolution generally, for they are themselves an end-station on one line of this evolution, too highly specialized and too well adapted to be easily susceptible of great change. But they have established for themselves a place in nature that is not likely to be challenged, short of profound changes in the environment and perhaps even the end of life itself upon this planet. In general we may be glad that this is so, for birds have become an important ecological unit in our human world, as destroyers of insects and other pests, as scavengers of waste, as food, and as among nature's most attractive ornaments. The world would indeed be a drearier place without them.

Mammals: The Highest Vertebrates

Some 150 million years or more ago, even before the great age of the dinosaurs, there lived a reptile with startling mammal-like characteristics, presaging the rise of the group which today represents the culmination of animal evolution. This creature — *Cynognathus*, the “dog-jawed” (page 130) — probably looked like a combination of a dog and a lizard. It had a varied assortment of teeth, like a mammal, and in the position of its limbs it was far more efficient than its sprawling ancestors. The elbow had moved back and the knee forward, so that the legs now became supporting pillars. Moreover, certain features of mouth and nose structure, which made uninterrupted breathing possible, even suggest that the creature may already have evolved a degree of warm-bloodedness.

A dozen million years later, in the very heyday of the giant reptiles, real though still primitive mammals tentatively embarked on the journey that led to man. These creatures were at first insignificant pygmies, and no match for the giant reptiles that still flourished in the lushness of the Mesozoic climate. The delicate fragments of jaws and teeth which are the only surviving records of these first mammals give no hint of their tremendous evolutionary possibilities. Hunted and repressed, these potentialities could not blossom until a more rigorous climate had laid their reptilian overlords low. But today there are some 3500 living species of mammals. They are more adaptive and generally more abundant and widespread than any other vertebrate class of land animals, with the exception of the birds. But the birds are perhaps too narrowly specialized to make the same bid for long-term survival that is so evident in the mammals. No other group can compete

with them in intelligence, that is, in the ability to learn and to reason. And no other quality brings with it such possibilities.

They were not always so. Here as elsewhere, evolution did not at once blunder onto a perfect answer. In a first exuberant burst of diversification, begun perhaps in the Cretaceous Period and blossoming in the Eocene, there evolved a group of archaic mammals which appeared successful enough. This included the creodonts, a flesh-eating group, which promptly followed the evolution of suitable prey, such as the archaic ungulates or hoofed animals, the condylarths. These developed increasing speed as their pursuers evolved. Other herbivores claimed survival for a time by increasing in size until they became grotesque, lumbering creatures of elephantine proportions, while their brains remained dull. Most of these first mammalian achievements succumbed under the competition of newer, more adaptive and especially more brainy forms, and by the end of the Eocene, they disappeared from the scene, for now the progenitors of the modern mammals had made their appearance — modern hoofed animals, such as horses, rodents such as rats, and even primates, representatives of the group which spawned man.

All mammals are characterized by the possession of milk-producing glands (*L. mamma* = breast) and by a body covering of hair. No other animals have these characteristics. In addition, all mammals, like birds, are warm-blooded or, more specifically, even-temperatured. Except for the small and primitive group known as monotremes, whose members still lay eggs, they all bear their young alive. All mammals breathe by means of lungs, and they alone possess a bellows-like diaphragm

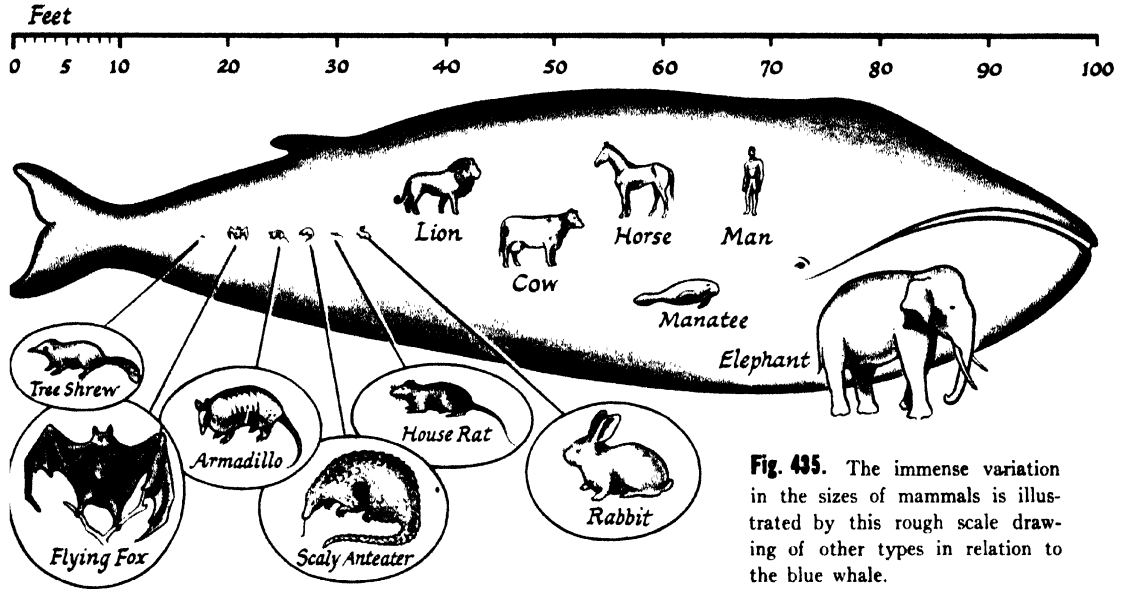


Fig. 435. The immense variation in the sizes of mammals is illustrated by this rough scale drawing of other types in relation to the blue whale.

with which to inflate them. Four legs are characteristic of mammals, though in some cases these are rudimentary. There is always a four-chambered heart and a double circulatory system, similar to that of birds, but of unique mammalian design. The red blood cells are usually without a nucleus, and thus have a short if efficient life span.

Probably no other animal group covers a wider range in size than the mammals, from the minute shrew to the largest animal that ever lived, the whale (Fig. 435). Mammals also cover a wider range of adaptations than any other modern animal, for they are found literally wherever there is any life at all. Whales penetrate thousands of feet below the ocean's surface. Moles burrow beneath the ground. Foxes and bears live in the far Arctic, and foxes, rats, and hares inhabit deserts. In the bats, mammals have even invaded the air. The three main groups of mammals show a distinct rise from more primitive to more advanced forms, especially in their embryology.

TYPES OF MAMMALS

Primitive Mammals

In Australia and the neighboring islands, a land area cut off in the earliest Eocene from

other parts of the earth where higher mammals developed, there still survive two types of primitive creatures belonging to the simplest of the three chief mammal groups, the order *Mono-tremata* (L. *mono* = one + *trema* = opening), so called because of its combined urogenital and intestinal opening, the cloaca. The now famous duckbilled platypus (Fig. 436) is a member of this group, as is the spiny anteater. These creatures lay eggs with large yolks, like the reptiles, and they have horny beaks like birds. A common cloaca is also a feature similar to that of reptiles and birds. They are warm blooded, though less constant in temperature than most mammals, and they have a body covering of hair. There are mammary glands but no teats, and the young suck or lick the milk from the glands on the abdomen of the mother. All these traits suggest that these mammals, despite their specializations, are conservative survivors of a group that may have been transitional between the reptiles and the higher mammals. Particularly interesting is the fact that they have survived only in an area where they have been altogether free of the competition of the more efficient placental mammals, who appeared on the other continents only after their isolation from Australia.

The Marsupials

Intermediate between these egg-laying mammals and the "true" or placental mammals is a relatively rich and varied group known as marsupials (*L. marsupium* = pouch) since their young, though born alive, are carried during a developmental period in a pouch on the abdomen of the mother. Perhaps as early as the upper Triassic, perhaps somewhat later, there came this second offshoot of the basic mammal-like reptilian stock, which, evolving in its own separate way, gave rise to the modern marsupials. Today they are the characteristic mammals of Australia and neighboring islands, among them the kangaroos (Fig. 437), wombats, and koalas.

A few marsupials — notably the American opossum — have survived in other parts of the world. The group once flourished in South America, but invading hordes of placental mammals from the north soon eliminated all but a few of them, when the North and South American continents were joined. Obviously the marsupials were no match for their competitors. Why was this so?

The answer appears to lie mainly in the nature of the reproductive care given the embryonic young ones. Marsupials are characterized especially by the fact that the egg develops in the uterus, from the walls of which it absorbs a certain amount of food for a relatively short time. The young are born at a very immature stage and are then placed in the pouch of the



Fig. 437. A female kangaroo, showing the pouch in which the young mature after birth.

mother. A full grown kangaroo, which may weigh over two hundred pounds, has young that weigh but a few ounces at birth and are no larger than the last two joints of a little finger. They look extremely embryonic, translucent, and worm-like. When they are born, the mother places them against a teat in the pouch, and here they stay, literally grown fast to the teat, while they continue to develop. The absence of eggs and the nourishment of the young within the uterus before birth is a distinct advance in the direction taken by the higher mammals. Moreover, the unique pouch is undoubtedly of survival value, since thereby the young are carried by the mother until they develop their own independence and are not, like eggs, in danger of being left unprotected in moments of crisis. But the limited number of marsupials surviving today shows clearly that from the point of view of survival, their method of bearing and nurturing their young must have distinct disadvantages. The limited intelligence of the average marsupial is no doubt also a factor in their losing battle for survival.

The "True" or Placental Mammals

By far the most successful of the three subclasses of mammals, and certainly the most highly evolved, are the placental mammals, in which the young are nourished throughout their embryonic life in the uterus of the mother and are born alive. The overwhelming superiority

Fig. 436. The duckbilled platypus, a primitive, egg-laying mammal (a monotreme).





Fig. 438. The tree-shrew (*Tupaia lama*), an insectivore.

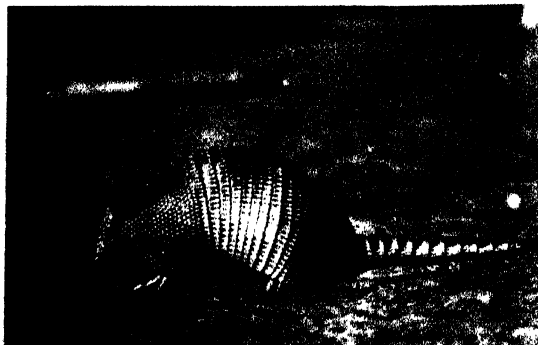
of this reproductive mechanism over those of the monotremes and the marsupials is evident not only from the fact that the lower forms thrive only in the absence of the higher, but also from the tremendous numbers of placentals in existence today. As against four species of monotremes and 150 of marsupials, there are about 3500 of placental mammals. Moreover, in size, form, variety, habits, habitat, and general domination of the environment, this mammalian group covers a far wider range than their lowlier cousins.

The chief reason for this superiority — the factor giving the “edge” which in the long run overwhelmingly increased the chances for survival — was probably the development of the *placenta* (Gr. *placenta* = a flat cake). This is a round, flat organ which is formed partly from the uterus and partly from membranes. One side of the placenta is attached to the wall of the uterus, through which it draws oxygen and nourishment and gives off carbon dioxide and the other wastes. The other side of it is attached to the embryo by the umbilical cord.

Because of the existence of this organ, the tremendous amounts of yolk which are required in egg-laying animals in order to nourish the embryo through a long period of development, are not necessary in mammals. Consequently the burden of the pregnant female, while considerable during the later stages, is compensated by a lower requirement for food. At the same time, the unborn young are protected in a way possible in few other animals.

In general the great variety of mammals is well known, although few except biologists could group them according to their outstanding characteristics. In the main mammals are land animals though there are notable exceptions, such as the whales, the manatee, the dugong, the seals and the walrus, which have returned to the water and by convergent evolution have taken on a superficial resemblance to the fishes. Limbs have become flippers, in appearance somewhat like fins, and the body shows some evidence of being streamlined like a fish. The bats, the only mammals modified for flight, also show some signs of convergent evolution, for they have become bird-like in some ways. On the basis of their feeding habits, land mammals may be crudely grouped into four main types: the carnivores are primarily meat-eaters; the ungulates or hoofed animals are herbivores; the rodents or “gnawers” live on a mixed diet; and the insectivores eat insects and other small creatures, as their name implies. The whole group is generally divided into about thirteen main orders (see Appendix A for further details). Since most of the animals one generally sees are placental mammals, the group holds particular interest for us.

Fig. 439. The giant anteater, an edentate, is one of the more grotesque of mammals. The armadillo, a near relative, is a contender in oddity.



Principal Mammal Groups

The first mammals appear to have resembled the *Insectivora* most closely among modern mammals, and these may therefore be considered to be a sort of mammalian prototype. Some insectivores, such as moles and hedgehogs, are very specialized. Shrews are more typical. They are generally very small creatures, often somewhat mouse-like in appearance, but with many needle-like teeth suitable only for catching such small prey as insects. Among them are the tree-shrews, some of which are less than two inches long (Fig. 438). Many insectivores are still arboreal, as the first mammals probably were.

In the order *Edentata*, or "toothless" mammals, there are some extraordinary animals, such as the giant anteater (Fig. 439), the armadillo, and the preposterous-looking sloths. The latter spend their lives suspended upside-down, hanging by hook-like claws from branches. They never descend to the ground unless forced to do so, and when they do, they flounder about as helplessly as though every bone in their bodies were broken. Survival for these highly specialized creatures depends entirely on remaining unseen, for their movements are inordinately slow. Their intellect is extremely low. Their evolution towards self-effacement is climaxed by the dull green color of their fur, brought about not by their own pigments, but by symbiotic algae which live in unique groove-like structures of the hair that seem to have evolved specifically for this function. Most edentates have teeth reduced in size and number, without any enamel, and they have no incisors. The giant anteater has no teeth at all, and feeds on ants and termites by means of a long sticky tongue which it protrudes from its slender proboscis-like muzzle.

Of all the mammals, only the order of the *Chiroptera*, or bats, has evolved true flight (Fig. 440). Probably offshoots of early insectivores, many bats are still insect-eaters, though the "flying foxes" or fruit-eating bats have become entirely herbivorous, and there are a few blood-sucking bats. Their power of flight is accomplished by thin skin stretched across



Fig. 440. The bats and the "flying-foxes" are the only mammals adapted to flight. The animal here shown is a bat.

enormously elongated fingers, in structure somewhat like an umbrella. They have an amazing ability to avoid hitting obstacles while in flight, even in the dark, and dodge skilfully through the twilit sky as they chase elusive insects.

Perhaps the least mammalian in appearance of all mammals are the scaly anteaters of Asia and Africa, members of the order *Pholidota*. Though they are related to the hair-covered giant anteaters of the order *Edentata*, and although they eat the same food and secure it in the same way too, these creatures are covered with a rustling armor of horny scales, reminiscent of reptiles, though it has probably not been inherited from these. Some doubtful remnants of this group have been found in Oligocene deposits, but they are probably an old and isolated stock, and their relationship is doubtful.

For numbers of individuals as well as of species, the grand prize must be awarded to the *Rodentia*, or the "gnawers," for every single rodent family that evolved at the beginning of rodent history in the Eocene Period is still with us today. Generally unspectacular in appearance, these persistent pests have been more than able to hold their own in the midst of man-dominated territory, for these are the only too familiar rats, mice, gophers, woodchucks, squirrels, chipmunks, and muskrats. Other rodents, such as porcupines (Fig. 441) and beavers, have not been so successful in adjusting to man's presence, despite, or perhaps even because of,



Fig. 441. A porcupine, a rodent.

the unique specializations that made them very successful in their original unmolested habitat. The flat paddle-tail of the beaver, his enormous tree-felling chisel-teeth, his large size and notable engineering instincts, helped him little in his struggle for survival against the trapper. The modified hairs of the porcupine, which form an impregnable barricade, and even an offensive weapon, against tooth and claw, offer little defense against arrow and shot. The apparently defenseless small rodents, the rats and mice, and their larger burrowing cousins the gophers and woodchucks, have a much better chance for survival. The secretive instincts of these prowlers, coupled with phenomenal fecundity, catholic tastes in food, and considerable intelligence, makes them tough competitors of man. Especially characteristic of the order are the peculiar self-sharpening, chisel-like incisors, which give these creatures their name. Rabbits and hares, although often classified as rodents, have little other than their gnawing teeth in common with them, and are probably more accurately grouped in their own order, the *Lagomorpha*.

As relatively defenseless progenitors of modern herbivores evolved, small and relatively brainy ancestors of our modern carnivores appeared on the scene. These were the small and probably arboreal miacids (see page 137), from which presumably there evolved the varied

host of modern *Carnivora*, to partake of the plentiful supply of herbivore flesh. Today this diverse assembly includes the dogs, cats, skunks, minks, bears, foxes, and many others. Some are still, or have become anew, more or less omnivorous, and even such typical carnivores as foxes know how to enjoy sweet, ripe berries in season. All carnivores are characterized by having well developed canine teeth, useful in tearing flesh, while their incisors are small. Shearing molars are adapted to a meat-chopping function. In many carnivores, also, well developed claws have become powerful and dangerous weapons, effective in the capture and killing of food. The aquatic *Pinnipedia*, the walruses, seals, sea-lions, and sea-elephants, probably arose from the same miacid stock as an aberrant offshoot that went back to the sea, and they are often classified in the same order with other carnivores.

Among the two orders of modern ungulates, all of them herbivorous, the odd-toed stock, or *Perissodactyla*, began their evolution first, and gave rise to such modern representatives as the horses, tapirs, and rhinoceroses. But these are the last survivors of the order, and they too seem to be on the way to extinction. Man, to be sure, may save the domesticated species for a while. But gone are the once mighty giant rhinoceroses, such as *Baluchitherium* (page 137), whose shoulder height was 18 feet. These odd-toed ungulates are distinguished from the even-toed group in that the axis of the foot passes through the third or middle digit, while one or more lateral digits have disappeared. Thus the rhinoceros has three toes on each foot, the tapir four toes on each front and three on each hind foot, while the horse, with but one toe left on each foot, has carried toe reduction to its ultimate conclusion.

In contrast, the even-toed ungulates, comprising the order *Artiodactyla*, have the axis of the foot passing between the third and fourth digits. This produces a "cloven hoof," as in goats, cattle, sheep, and pigs. Although the *Artiodactyla* started their burst of evolution later than the *Perissodactyla*, they soon outdistanced them, and gradually became the

dominant herbivores. Yet only two groups have survived to the present day — the ruminants or cud-chewers, including the camels, sheep, cattle, and goats, and the pig-like ungulates, the pigs, peccaries, and hippopotamuses.

The greatest in size of land mammals are the *Proboscidea*, represented today only by the elephants of Africa and Asia. The mammoths and mastodons, recently extinct relatives of the elephants, are scarcely gone from the scene, since a woolly mammoth, complete with flesh and hair, was found preserved in the frozen Siberian tundra but a few years ago. Most striking in this highly specialized group is the astonishingly elongated and muscular nose, or trunk. Few specializations exceed this structure in oddness, yet it is a versatile instrument of almost as many uses as the tentacles of an octopus. The upper incisors, greatly enlarged to form tusks, are still in demand as a source of ivory.

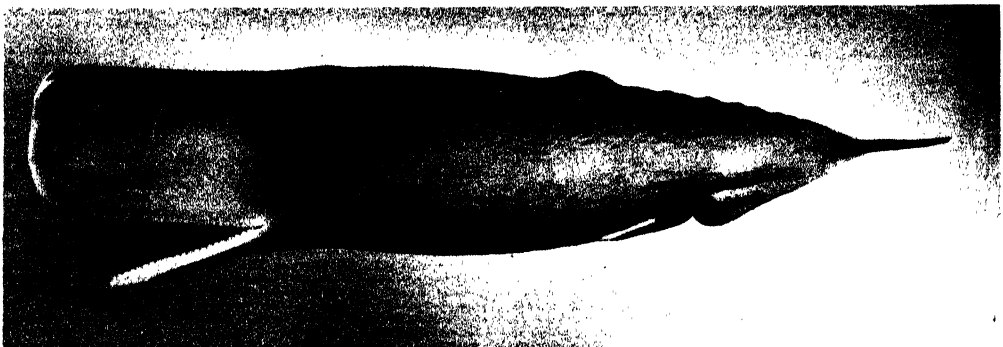
Branches of the same family tree in the early Eocene became the *Sirenia* of today, showing but little outward evidence of their relationship to the elephants. These are the sea-cows, the dugong and the manatee, dull aquatic herbivores, feeding on the abundant submerged vegetation of tropical streams and seas. While they resemble their mythological namesakes in form and habitat, their charms are distinctly open to question, from a human point of view.

No mammals have so completely readapted themselves to aquatic life as have the *Cetacea*,

the order of whales and porpoises. Though much less fish-like in appearance when they first appeared in the middle Eocene, they had obviously already had a long period of adaptation to marine life behind them, for they had even then passed that intermediate stage of marine adaptation which we find today in the seals. Possibly descended from primitive creodont fish-eating ancestors, they have had a long isolated evolution. No animal of the present or past has ever approached the modern monsters of this order in size — the sulphur-bottom whale may attain a length of over 100 feet. Modern whales form two groups — the toothed whales and the whalebone whales. Although all of them have teeth in the early stages of life, the whalebone whales soon replace them with parallel plates of whalebone depending from the roof of the mouth. These serve as strainers in securing the food which, rather oddly for creatures of such enormous size, consists of the minute plankton of the ocean.

Last to be discussed here is the order of the *Primates*, which includes not only lemurs, tarsoids, monkeys, and apes, but also man. Although the familiar members of this group are generally thought of as the “highest” of all animals, they are in many ways surprisingly primitive, inasmuch as they lack highly specialized structures such as the hoofs of the ungulates, the gnawing or tearing teeth of rodents or carnivores, or the proboscis of the anteater or the elephant. Instead, they still have the

Fig. 442. The sperm whale. Note the vestigial limbs and the tail.



five original digits on all four of their limbs, together with only moderately specialized incisors, canines, and molars, and a rather underdeveloped nose. Tree dwellers from their earliest appearance onward, with but few exceptions, their fossils are rare and our knowledge of their evolution is far more spotty than we would like to have it. Like all other mammals, they are probably descendants of early arboreal insectivores, and apparently simply continued their evolution as arboreal forms. Not until Eocene times, however, were fossils of recognizable primates preserved.

Like other mammals, most primates have tails, though baboons, apes, and man do not, except in rare but notable cases. Thus, in the majority of their features, they have evolved along the middle of the road, with a single but profound exception — their brain development. In this respect their advances have been meteoric, and parallel with this has been the evolution of the hand, not so much in its external appearance as in its innervation and muscular equipment. Freed from use in locomotion by upright posture, at first only intermittent, the hand became a uniquely efficient organ for grasping and manipulation.

Mammalian Relationships

The specific relationships between the orders of mammals are rather obscure, and frequently reach back far into the early Eocene or even the Cretaceous Period. Indeed, no mammalian orders have common ancestors more recent than fifty million years ago, and ever since that time their evolution has followed divergent, parallel — or in some cases, convergent — evolutionary paths. The monotremes and the marsupials branched from the mammal-like reptile stock probably as early as the upper Triassic. Among the later placental mammals, only a few distant relationships are apparent. It is probable that the bats, primates, and insectivores are all offshoots of primitive insectivore stock. Oddly enough, the whales also may be descended from the same branch. The modern carnivores were descendants of another obscure group, the miacids, which were probably tree

dwellers. Earliest ancestors of the horse-like ungulates showed structural relationships to the carnivores, whereas fossils of other primitive ungulates show such evident affiliations to insectivores, and even to the primate stock, that they were at first classified with these. Another offshoot of the earliest undifferentiated ungulate stock produced the elephants and their relatives, and from this group in turn came the sea-cows. The rodents, most numerous of mammals, have a long independent history. Thus each of the mammalian orders branched off more or less separately from primitive mammalian stock, producing many minor variants along the way. Generally, however, no modern order can be considered ancestral to another.

THE PRIMATES

We now focus upon one remote branch of the complex evolutionary tree, that of the primates the order which has produced a most spectacular creature, man. Other twigs on the same branch, however, are the dog-faced, pack-hunting baboon, the formidable gorilla, and the fragile *Tarsius*. The order has been given its name presumably because it includes man, who represents the highest achievement to date in intellectual development, although it is not too difficult to visualize further progress.

Distinguishing Characteristics

The primates possess no striking features such as gnawing teeth, hooves, horns, fangs, or claws. Indeed the lowest members of the order might pass for primitive carnivores or advanced types of the insectivores from which they sprang. In trying to characterize the primates, we grapple again with the ever recurring problem of finding sharp divisions within a continuum. Yet certain common features appear throughout the members of the order, and most of them trace back to the changes wrought by selection for the arboreal life begun by the earliest members of the group and still common to many. Opposable digits enable the hand or foot to grasp a branch, and the claw is reduced to a flat nail. In most orders of mammals the clavicle, or collar bone,

is reduced or quite absent, but in primates it is well developed, serving as a brace for the shoulder, and very useful in swinging by the arms or walking along branches. No single feature, however, trade-marks the order. Bats, for example, also have a similar clavicle. When we think of primates we think of brains, and in this we are justified, for no other organism equals the higher primates in brain development. Yet the lowest primates are intellectually inferior to many species of other orders.

The Typical Primate

Contrary to the popular concept, the primate is generally a timid creature, not greatly changed from the least specialized of mammals, the insectivores. The typical primate is semi-nocturnal, and when it ventures abroad by day, it favors shadowed places where it can quickly vanish into the tangled foliage of the thickly wooded areas it prefers. Insects, fruit, and eggs compose the bulk of its diet. In contrast with the most advanced members of its order, it is still a quadruped and runs along branches on all fours, clinging to them with its opposable digits. The emancipation of its hands from use for locomotion is foreshadowed in its habit of sitting on its haunches and using the hands for manipulating food.

A long snout, a low brow, a heavy coat of fur, and a long bushy tail are characteristic. Except in lemurs, the nasal region tends to be degenerate for lack of positive selective factors. The sense of smell is of doubtful value to a tree dweller, for the broken trail of an animal leaping from branch to branch would be of little use to a nose-guided creature.

In response to the selective forces of arboreal life, the eyes are frontally rather than laterally placed, except, once again, in lemurs. Thus perspective vision becomes possible, the fusion of overlapping images from both eyes producing the effect of depth. To a tree dweller the value of this form of vision in judging distances is obvious — as we can readily tell by closing one eye and trying to thread a needle or pour a cup of tea. The stereoscopic viewer for pictures also illustrates this principle.

The mammae or breasts of primates, unlike those of most other mammals, consist of a single pair in the pectoral or breast region. In some, an accessory pair may be situated in the groin, but these are functional only in lemurs. Even in man, supernumerary mammae may occur along the two parallel lines running from the groin to the armpits, reminiscent of the rows of teats in all lower litter-producing mammals. Retention of pectoral breasts in primates, rather than the lower ones, as in animals such as the ungulates, is correlated with the use of the forelimbs in the case of the infant, for holding it clasped to the breast probably favored the mammae of that region. Most primates produce but one — or rarely two — offspring at a time — another adaptation to arboreal life, for the pregnant female would be excessively hampered by too great a burden. Similarly, the prolonged care of the young after birth, so necessary in such an environment, would tend to limit the possible number to one or at most two. Thus, among primates, multiple birth is a primitive characteristic.

Range of Primates

With the exception of man, modern primates are limited to the tropic and subtropical regions of the earth. They are generally forest-dwellers, though baboons have reverted to the ground and live in semi-desert regions in northern and extreme southern Africa. The families of the primates spread round the world in a belt straddling the equator. In the western hemisphere they range as far north as Mexico and southward to northern Argentina and Uruguay; in the eastern hemisphere, from southern Japan to the tip of South Africa. In earlier periods, primates probably had a much more extensive range, and we find fossil primates of the Miocene Period in Europe. With the increasing aridity of the Miocene, primates probably retreated along with the receding forests.

No modern primate can be considered ancestral to man (Figs. 452 and 453). All are distinct and specialized forms whose ancestors diverged from ours from 15 to over 50 million



Fig. 443. The Potto. A primitive lemuroid of Africa and Asia. Index finger is vestigial.

years ago. The earliest primate line, the lemuroids, emerged from that of the unspecialized insectivores somewhere in the Eocene, nearly 60 million years ago, at a time when this ancestor looked somewhat like the lemur of today. From this relatively plastic line specialized forms branched off from time to time, while the main stock remained relatively unspecialized. Each of the branches seems to have become set in its particular specialization, and finally the basic line appears to have culminated in man. It is not likely that new or divergent varieties will arise out of the advanced forms.

The Lemurs

Primates are of three main types, the lemuroids, the tarsoids, and the anthropoids. The lemurs and the tarsiers have been called the "poor relations" of the primate order, for they possess few of its more highly developed characteristics. Lemurs are most abundant on the island of Madagascar — and limitation to an island refuge is generally indicative of backwardness, for lack of competition. Lemurs are fox-like in appearance, with long snouts, long bushy tails, and inferior intelligence; and they are nocturnal in habit (Fig. 443). They are arboreal, and omnivorous in diet.

The Asiatic lorises, a subdivision of the lemuroids, show some advance in body structure. They have digits specialized for grasping, and the snout is markedly reduced. The advance of the loris over the lemur may mirror its greater insecurity. The lemur is typically

ultra-conservative, and the direction of its evolution promises no future. In contrast with many tree-living animals, some lemurs, especially the loris, move with well nigh unbelievable caution. Minutes may elapse between movements in such activities as climbing, and only in the tree tops in a land where it has few enemies could such a lethargic animal exist. Its bid for survival seems based primarily on two factors. First, the animal could not possibly fall, since at any given moment at least three of its feet securely grasp a limb, and it never lets go with one foot before the fourth has secured anchorage. Second, the animal moves so slowly and infrequently that its potential enemies would have difficulty in recognizing it as being alive. Other lemurs are as active and agile as any monkey.

Tarsius

In the middle of the Eocene Period, another split in the basic primate stock led to the tarsoids, a group which has dwindled until today it is represented only by *Tarsius spectrum* (Fig. 444). About the size of a rat, this crea-

Fig. 444. Tarsius. Close to the main line of man's descent?



ture has a short compact body, long legs and tail, and a round head. The hind legs have become specialized for hopping by the elongation of the heel bone, a unique development which permits the retention of a grasping organ at the end of a hopping foot. The snout is greatly reduced, the eyes are shifted toward the frontal plane, and there is a complete bony orbit around the eye, as in higher primates. *Tarsius* is primarily an insect eater, catching its prey by lightning-like pounces. It is completely nocturnal and arboreal, timid, and very rarely seen.

This small recluse has become the center of considerable dispute among anthropologists. One group maintains that it is descended from an undiscovered generalized ancestral tarsiod which gave rise to the anthropoids and man, while the other believes that even the most ancient fossil tarsiods are far too specialized to be on the main line of ascent to the higher primates. There may be truth in both views, for it could be that a still earlier generalized ancestor of *Tarsius* may have been on the main line.

Fig. 445. A divergent, specialized New World monkey *Ateles*, the spider monkey. Note the prehensile tail



Fig. 446. Another specialized monkey, the howler, *Myiotes*.

The Anthropoids

All primates above the tarsiers belong to a single related group, the anthropoids. This order includes the monkeys, two families in the New World and one in the Old. Monkeys are the most widespread of all primates except man, and compose the greatest number of primate species. No modern kinds of monkeys, however, are direct ancestors of man, and it is thus incorrect to say that man descended from them. Rather, they are a highly specialized side branch in their own right, interesting because of their peculiarities of behavior and appearance, though for many they are an affront to vanity, for in the light of evolution it is quite correct to say: "There, but for the grace of chance, go I."

The New World Monkeys

Of this group two members are outstanding examples of divergent specialization. The first is the spider monkey, *Ateles* (Fig. 445), one of the very few monkeys to brachiate, that is, to swing hand-over-hand through the branches. This is a mode of progression generally reserved to the apes, and we may thus more easily see how the transition from quadrupedal monkeys to almost bipedal apes occurred. *Ateles* is also one of the rare monkeys with a prehensile tail, all of them limited to this American group.

The second peculiar specialist in this group is the howler monkey, *Myiotes* (Fig. 446). The howler is named for the unusual development



Fig. 447. A divergent Old World monkey, the baboon (*Papio hamadryas*), re-adapted to terrestrial life.

of its vocal mechanism, which includes prominent bony resonators in the skull. Brain and voice appear to stand in some inverse ratio, a quality, however, not confined to *Myceles* among the primates. The howler is of even greater interest because of its unusual social organization. Howlers generally live peaceably in groups consisting of two or three males and about twice as many females. Jealousy and the exclusive possession of a female by a male, so prevalent among other primates, appear totally lacking in this American monkey.

The Old World Monkeys

Among these the baboon (*Papio*) is perhaps the most divergent and therefore perhaps the most interesting. This large, terrestrial, dog-faced monkey has again become quadrupedal, and is suggestive of what man might have become had his ancestors descended from the trees slightly earlier than they did and before they had become confirmed brachiators (Fig. 447). The baboon has evolved typically terrestrial limb-proportions. Front and hind legs are of approximately the same length, and the animal walks on the balls of its feet and on its "hands." Though brutish and stupid in appearance, and often truly frightful of expression, the baboons appear to be really intelligent. They seem able to cooperate well within their social group, especially under the pressure of

outside danger, and generally do not attack others who do not bother them. But they are dangerous enemies and fight fiercely when molested. Their highly organized raids on orchards and farms bring them into serious conflict with advancing civilization.

The Great Apes

The New World monkeys split off from the common stock somewhat later than the lemuroids and the tarsiods, but still in the Eocene Period. A fossilized jaw of a primate called *Parapithecus* found in Oligocene deposits represents this generalized-monkey phase of primate evolution. But the ape-like jaw of the miniature *Propliopithecus*, found at the same level, indicates that apes left the main line at an early stage, and did not long remain in the generalized monkey stage. Thus it was in the Oligocene, more than twenty million years ago, that the anthropoid apes turned their aristocratic backs upon the monkeys and began their upward climb. But it may be noted that they also turned their backs upon the stock that led to man.

Fig. 448. The smallest and most highly specialized arboreal great ape, the gibbon, *Hylobates*.

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The great apes include the gibbons, the orang-utan, the chimpanzee, and the gorilla, though it is especially to the last three of these that the name is generally applied.

The Gibbons. The gibbons (Fig. 448) are restricted in habitat to the Malay peninsula and nearby islands. Completely and probably irrevocably adapted to arboreal life, a gibbon rarely comes to the ground, even to drink. This slender, spidery creature is rarely over three feet tall, and with its greyhound waist, is extremely light even in proportion to its height. Its arms are enormously long, and because the legs are somewhat shorter, the arms can easily be rested on the ground even while the animal stands. They have become so completely adapted for brachiation that their thumbs are reduced to stumps and the fingers and hand itself are elongated to form hooks by which to hang. On the ground gibbons walk with a hopping gait and with arms elevated, but in the trees they swing themselves along by a series of spectacular leaps which may span as much as thirty or forty feet. Despite its small size and grotesquely long arms, the gibbon resembles man more closely in certain other respects than does any other ape. It is closest to man in the relative length of leg and trunk and in the proportions of its facial skeleton and of brain to face. Its ability to walk upright is exceeded only by man's.

In spite of these similarities, the gibbon is not generally considered a close relative of man, though one group of anthropologists consider it man's closest non-human living relative. It has thus been suggested that human stock emerged at about the same time the gibbon split off, and that the small proto-human took to the ground while the gibbon stayed in the trees. But differences in tooth pattern — an important measure of relationship — divergence in the proportion of arm to body, and the questionable survival ability of so small a primate on the ground, have all been cited as reasons against this view.

The Orangutan. This picturesque name — Malay for "man of the forest" — is given to an animal entirely worthy of it. More re-



Fig. 449. An infant Orangutan shows greater similarity to man than does the mature animal.

stricted in range than any other ape, the orang-utan is found only in the northern tip of Sumatra and on Borneo (Fig. 449). In its own peculiar way, the orang is quite as well adapted to arboreal life as the gibbon, but where the latter is light and swift, the orang is heavy and moves with extreme caution and deliberateness. Its arms are immensely long and powerful, with long specialized hooking hands and reduced thumbs. The legs are pathetically weak and small, and the foot wholly modified as a grasping organ. Walking on the ground is an awkward and apparently painful process for the orang, who gives much the impression of a man on crutches. The temperament of the animal fits its cautious movements. The recollection of its gleeful grin or laugh, as it finds a nest full of bird's eggs, is an unforgettable reminder of this ape's closeness to us in its emotional capacities.

Chimpanzee and Gorilla. These are the African apes and are considered somewhat



Fig. 450. Young chimpanzees show surprising dependence on one another.

closer to human evolution than their eastern relatives. Both chimpanzee and gorilla are restricted to areas in the most densely wooded sections of central Africa. The chimpanzee (Fig. 450), which has been studied more extensively than any other ape, has become quite successfully adapted to life, and even to reproduction in captivity. Only partly arboreal, it still brachiates very well, but it prefers to spend a large part of its time on the ground, possibly because of its considerable weight. In overall body proportions, the chimpanzee is closer to man than any other ape. Its maximum height is about five feet and its greatest weight about 175 pounds. Since its arms represent a far larger proportion of its weight than do the arms of a man, a chimpanzee is a most formidable adversary. Like most apes, the "chimp" is playful, affectionate, and curious when young, but tends to grow reserved and morose, and is often unpredictable of temper in maturity. After man, the chimpanzee is probably the most intelligent of animals. It learns to use tools and is capable of solving problems of astonishing complexity. For example, one chimpanzee was given two bamboo poles, neither of which was long enough to

reach a coveted object. The animal solved the problem by inserting the end of one pole into that of the other, thus making a single instrument long enough to reach and secure the object. Yerkes, a leading primatologist, believes that the gorilla may exceed the chimpanzee in mental capacity, but both gorilla and orang are difficult subjects, for they are rugged individualists and do not take kindly to the "non-sense" of the psychologist.

The gorilla is without question the most impressive of the apes. An enormous and ponderously powerful animal, a full-grown male may stand a full six feet and tip the scales at 450 to 550 pounds (Fig. 451). The animal is still more impressive when we consider that in spite of its great digestive capacity, it does not tend toward obesity and that its legs are relatively short and weak. Thus the body of a mature gorilla is comparable to that of a stocky ten-foot human being, and its feats of strength fully match its proportions. Because of its great weight, the gorilla lives on the ground, although it still clings to the arboreal habits of its ancestors at bedtime. To prepare its bed for the night, it builds a nest of twigs pulled together into the low crotch of a tree. Among the primates, the gorilla ranks second to man in adaptation to life on the ground, and despite its return to the quadrupedal locomotion of primitive primates, shows some adaptation to upright posture in foot structure, especially in having an incipient heel.

The gorilla far surpasses man in length of arms in proportion to height, in general muscular development, and in jaw development. But a comparison of the skulls of a man and a gorilla shows in man a striking shift of relative size from muzzle to brain case.

The Golden Age of the Primates

Fossil records show that during the Miocene the anthropoids ranged throughout Africa, India, and China and penetrated Europe as far north as Germany. The mild climate, moderate moisture, and widespread forests of the early Miocene appear to have been ideal for them, and fifteen different genera have been

distinguished from that period, where there are but four today. One of the most successful was *Dryopithecus*, which covered almost the entire anthropoid range. Its success is of interest because this ape was probably ancestral to the great apes, if not to man.

Somewhere about this time what may have been an important step in human evolution was first taken, the development of brachiation, swinging by the arms. Such locomotion would favor by natural selection an anatomy pre-adapting the animal to upright posture. Semi-upright postures have been attained by the lower primates, but they still walk on all fours and thus are still basically quadrupeds. But in swinging by the arms, the body hangs perpendicular. Once the animal has evolved a body suited to this position, it naturally tends to maintain a similar position while walking along a branch — perhaps, like the gibbon, using its hands for support on higher branches.

But, we may ask, if brachiation predisposed man's ancestors to walk upright on two feet, why did it not do so for the chimpanzee and the gorilla, who also have in varying degrees returned to the ground? It has been suggested that these animals were too heavy to walk upright when they finally came down out of the trees, and that their skeletons were already modified. The modern great apes, in other words, have brachiated too long. But all this is merely speculation. There are still great gaps in our knowledge of such matters.

The Great Depression

During the latter part of the Miocene Period, mountain building brought a colder, dryer, and more exacting climate. The soft living of the Oligocene came to an end in many parts of the world, and selection, long postponed, now increased in rigor. As forests receded to the south and were replaced by park-like scatterings of trees, tree dwellers had to adapt themselves to at least temporary life on the ground or perish. Many did not adapt, and fossil records tell the story of many exterminated genera of apes. It was a slow process, and even if there had been human observers to

watch it, the selection and elimination must have been almost unnoticeable, certainly not violent. There would have been no evidence of a catastrophe. But these were long-continued hard times, and at the end of them, only the hardy had survived in the affected regions of the world.

FOSSIL ANCESTORS, DIRECT AND INDIRECT

It was during the million years of the Pleistocene Period that man's body and mind slowly evolved toward their present form and stature. This was a period of great climatic fluctuations, often referred to as the great Ice Age. But it was not a time of uninterrupted cold, for there were at least four major glaciations during which the polar ice cap crept into northern Europe and America, while southern glaciers spilled out of their alpine valleys to meet it. The invasions were gradual, and it could hardly have dawned upon the feeble intellect of early man that he was experiencing a change of climate. The glacial periods were relieved by longer interglacial ones during which conditions were probably as mild as

Fig. 451. An adult male gorilla, "Massa."



those we experience today or even milder.

The first two glacial invasions were separated from the last two by a long interglacial period, while briefer intermissions separated the first from the second, and the third from the fourth. In Europe the glacial periods have been named after Alpine valleys in which the stone deposits of their retreat are well shown. They are the Günz, Mindel, Riss, and Würm. Each glacial period appears to have lasted about 100,000 years and the "Ice Age," a million years in length, therefore actually included more temperate periods than cold ones. It is not certain to what degree the repeated glaciations influenced the evolution of man. *Eoanthropus* (the "southern ape") and *Sinanthropus* are generally supposed to have lived in the very long mid-Pleistocene glacial period. Only Neanderthal man is definitely known to have felt the direct pressure of a glacial climate.

The "Southern Apes"

The story of man's evolution is only sketchily charted. Fossilized primate skeletons are rare, and every new one found must be considered an unusual stroke of luck. One new-found relative of man is *Australopithecus*, the "southern ape," unearthed in South Africa (Fig. 452). The first find, in 1925, consisted of the incomplete skull of an infant of about five years of age, and later there were found two adult skulls, and remarkably human arm, leg, and toe fragments presumed to belong to these apes. Although these remains were found in late Pliocene or Pleistocene deposits, the branch must have diverged from the main line of human evolution considerably earlier. Indeed, the three skulls found provide an excellent candidate for the missing link, for they possess features of man, of the chimpanzee, of the gorilla, and of the orang, and such a mélange of characteristics is to be expected in a creature near the main stem of human evolution.

The "southern ape" had a brain capacity estimated as ranging from 440 to 733 cc., in the upper range considerably exceeding that of a modern gorilla (459 to 549 cc.). The admittedly human *Sinanthropus*, who had a brain volume

of 1075 cc., does not exceed that of the "southern ape" by too great an extent. While the face of this South African ape was probably concave and the jaw protuberant, the teeth were humanoid and the brain development suggests that the creature had started on the road toward man.

Pithecanthropus

Pithecanthropus erectus — the "erect ape-man" — is well named, although if Eugene Dubois, who found his fossil skull-cap on the banks of the Solo River in Java in 1890, had known the furore that it was to arouse, he might have added "earth-shaker" (Fig. 452). Only nineteen years had passed since Darwin had written *The Descent of Man*, and feeling still ran high over the question of man's anthropoid descent. Up to this time the stout opponents of such ideas had taken heart in the fact that no forms clearly intermediate between man and ape were known to exist. There were fossil human remains, such as man of Neanderthal, but they were sufficiently human to be accepted without too much question. *Pithecanthropus*, on the other hand, was embarrassingly rich in anthropoid characteristics. His brain capacity was only 900 cc., and his brow ridges were prodigious. On the other hand, he walked upright, as indicated by a thigh bone found nearby, and supposed to be his. Crude stone implements were found in the same strata. He had a very low brow, but perhaps he had acquired speech. The dispute over his authenticity lasted for years, but in 1937 Von Koenigswald, working in the same middle Pleistocene strata (about half a million years old), found skulls and leg bones of three other members of the same species — a veritable treasure trove — so that its authenticity and character can hardly be doubted any more.

Sinanthropus

Meanwhile anthropological interest had shifted to China, where in 1929 Davidson Black had discovered, in a cave broken and filled in since the mid-Pleistocene, the brain case of a

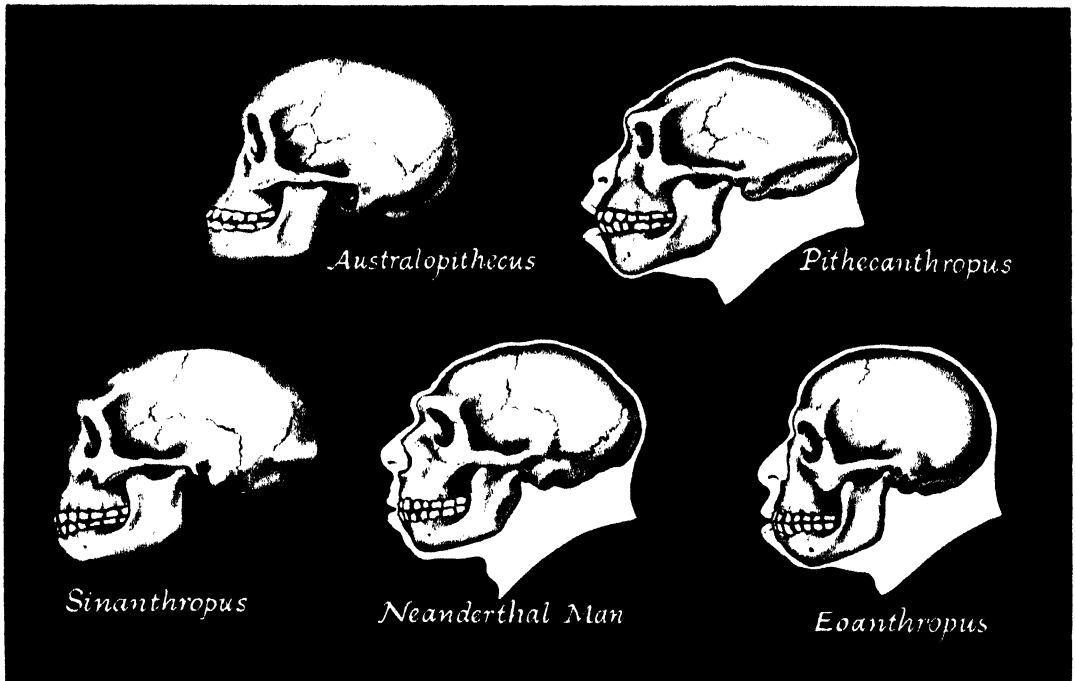


Fig. 452. Skulls and facial outlines of some ancestors of man, direct and indirect.

specimen much like *Pithecanthropus* but somewhat more advanced. By 1938 the collection of *Sinanthropus* individuals had grown to thirty-eight, an extraordinary number for a fossil race (Fig. 452). The cranial capacity of this human species ranged from 915 to 1225 cc., higher than that of *Pithecanthropus*. The jaw is less protrusive, though there is still a gap in the lower jaw into which the somewhat enlarged upper canines fit, a distinctly ape-like characteristic. But the femora of *Sinanthropus* show that he walked fully upright. In this respect he was more advanced than Neanderthal man, who came much later.

Probably *Sinanthropus* was directly descended from *Pithecanthropus* or from a closely allied form. He was a right-handed hunter who employed a variety of weapons made of sandstone, quartz, and chert. He lived in caves and used fire. Though exceedingly primitive, his way of life was not animal. It may be that the possibly less cultured *Pithecanthropus* continued an isolated evolution in the far south-eastern corner of the world and gave rise to

the Australoid of today. The more progressive *Sinanthropus* evolved under less restricted circumstances, and perhaps gave rise to the Neanderthal type of man.

Neanderthal Man

This is a very widespread late Pleistocene stock which was first discovered in Europe in 1856 — the earliest found fossil man, and perhaps the best known (Fig. 452). The species (*Homo neanderthalensis*) was prolific and widespread, roaming over much of Europe and even northern Africa and western Asia in the period of the last interglacial and glacial ages, 115,000 to 72,000 years ago. Despite a brain capacity of 1550 cc. — as high as that of most modern men or higher — he was quite ape-like in appearance. This is partly because of the peculiar conformation of his brain, weak in the frontal region but well developed in the occipital. He had huge brow ridges, prognathous jaws, and appears to have shuffled along with bent knees. His primitive culture, characterized by chipped-stone implements, is

known as Mousterian. He lived in caves and he buried his dead — a fact which suggests that he had some religious concepts. These practices account for the wealth of preserved material by which he is today represented. Although Neanderthal man was probably not an ancestor of modern man but an offshoot, a progressive branch of this genus does show advances in the direction of man as we know him. There are some indications that *Homo neanderthalensis* interbred with *Homo sapiens*, so that it is not unlikely that some of us may carry a few Neanderthaloid genes. Evidence for this suggestion comes from remains in caves at Mt. Carmel in Palestine, where a mixed group of skulls has been found which ranges from almost completely modern to typical Neanderthaloid. Those which show a blending of the two types perhaps indicate hybridization.

Eoanthropus

Eoanthropus, the “dawn man,” has been aptly named, for he is probably the earliest direct ancestor of modern man yet discovered (Fig. 452). The fact that “he” was probably female merits consideration. *Eoanthropus* lived in the early Pleistocene, or perhaps even in the late Pliocene, and was thus a contemporary of *Pithecanthropus*. The fossil remains were found in the terraces of the Thames valley about 1911 by an amateur anthropologist, Charles Dawson, and for a long time were regarded with some suspicion because of the apparent incongruity of skull and jaw. The skull is large for such an early specimen — at least as large as that of the average modern woman. But the jaw — that is another story. Massive and chinless, it has more the appearance of a chimpanzee jaw than of a human one. Indeed, for a long time authorities refused to believe that such a jaw could belong to such a skull. They felt, rather, that the jaw of a chimpanzee had been accidentally buried near the skull of a human being. But a recent find of a similar skull with the same type of ape-like jaw argues strongly that the two belonged to the same person. Yet, we may well

ask with anthropologist Hooton why such a combination should cause surprise, for we can hardly expect all parts of an organism to be equally “advanced” at the same time. The Piltdown woman — a name sometimes applied to *Eoanthropus* — was of the basic type which later spread over Europe and gave rise to many variant offshoots. Remains of a later date found in England include the Swanscombe and Galley Hill skulls, which have basic characteristics of *Eoanthropus* but more closely approach modern man in structure.

Homo Sapiens

Such types were the inhabitants of Europe during tens of thousands of years, and their physical characteristics changed very little. They were long-headed. Best known among them is *Cro-Magnon* man, of some 72,000 years ago, who is typical of the general development and state of culture of his time. The men of this group were hunters who used the stone spear and axe, and who may later have invented the bow. They probably wore skin garments, and today are famed principally for their cave paintings, some of which were startlingly realistic and very beautiful. They understood perspective, and could depict it with a skill not again equalled until the time of the Renaissance. Form and figure were emphasized by skillful shading, and certain tricks used by modern cartoonists were employed to give the effect of motion.

Two finds dating from the early period of *Homo sapiens* suggest the way in which the basic European stock differentiated into other racial types. One of these is the *Grimaldi couple*, found in a cave along the Riviera, and showing negroid characteristics in the skull and the thigh bones. The other is the *Chancelade skull*, found in south central France, which supposedly shows proto-mongoloid trends in conformation. During the Neolithic Age, which began in Europe about ten thousand years ago, a second type of man, a broad-headed type of unknown origin, appeared in Europe. These men mingled with the long-

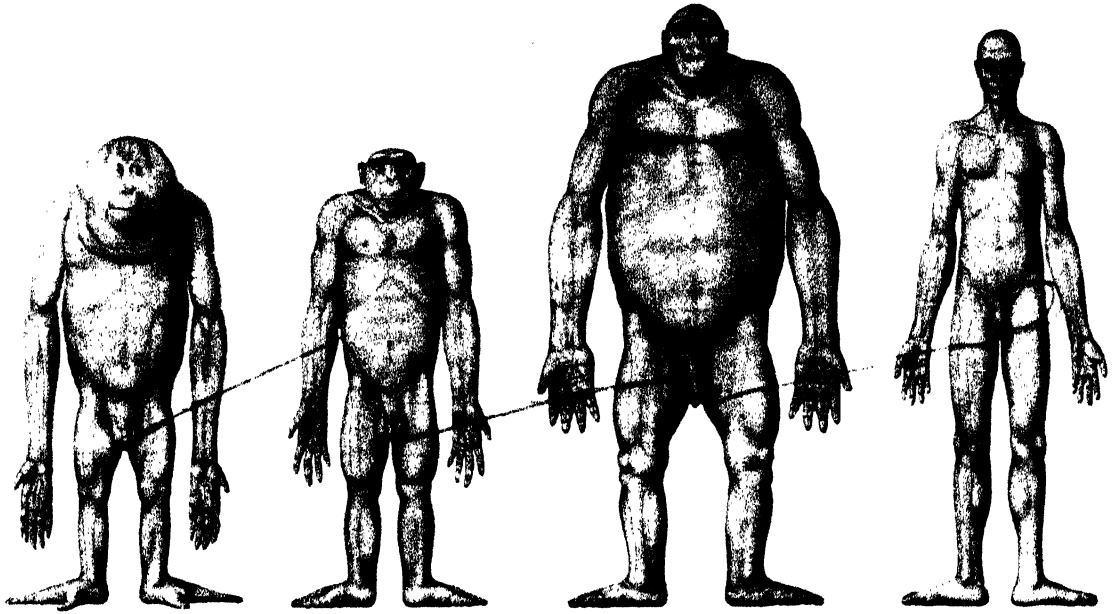


Fig. 453. Comparison of body proportions of man and the great apes. Orangutan, chimpanzee, gorilla, and man (Negro). (Drawings by Dr. Adolph H. Schultz.)

heads, producing the blending of types characteristic of present-day Europeans.

The Races of Man

The question whether mankind is a single species has caused considerable controversy, but complete interfertility among the races argues for the view that all men are of one species. The Australoid, however, is of such divergent descent that it might be justifiable to consider him a separate species. Customarily the divisions of mankind are given the status of races, and it is convenient to distinguish three, the white, the yellow, and the black, with certain generally distinguishing characteristics. A fourth, the Australoid, may be added. Traits considered primitive or ape-like appear in each, and in turn each is farthest removed from ape-like progenitors in other ways. Thus the negroid is most ape-like in degree of prognathism, but it is one of the least hairy and also least ape-like in the development of its thick, everted lips. The white race is least ape-like in being pale-skinned and orthognathous (straight faced), but it has most hair.

The typical mongoloid differs most from the ape in lack of brow ridges, general facial flatness, and lack of hair, but is most ape-like in blood groups (low O, very low Rh—). These primary races are divided into many secondary subraces, and all of them have intermingled in varying proportions to give rise to the more or less stabilized composite races of the present day.

The White Race (Caucasoid). Of the three main groups, the white race appears to be the most archaic, for it shows least divergence from the primitive types thus far found. This may, however, merely appear to be true because regions frequented by white stock have been most widely investigated. The distinguishing characteristics of the white race show a wider range than those of the other main races. Skin color ranges from pink to brown, hair from palest blond through dark brown, rarely black, and from straight through all degrees of waviness, but is never woolly and rarely tightly curled. Eye color ranges from blue through dark brown. Perhaps the simplest way to define the white race is to state

that it never shows the extreme forms of the characteristics that distinguish the others.

Within the white race a number of variant anthropological types may be distinguished, though these are not actual geographical sub-races or isolates, but rather represent only gene frequencies shared to various degrees by different populations and ethnic groups. The following such types may be named:

1. Mediterranean. Slender, small-framed, with dark wavy hair, dark eyes and skin. Common in Italy.

2. Nordic. Slender, tall. Blue or gray eyes, straight or wavy hair, ash blond, ash brown, or golden. Pink or ruddy complexion. Fairly common in parts of Germany and Scandinavia.

3. Celtic. Tall and slender. Light blue or gray eyes, wavy or curly dark or red hair, pale skin. Found in Ireland, Scotland, Wales.

4. Alpine. Short, stocky. Broad face, dark to medium brown hair, brown eyes, olive or brunette white skin. Most common in Switzerland and central Europe.

5. East Baltic. Short, stocky. Blond to light brown hair, blue to gray eyes, creamy skin. Found in Esthonia and Latvia.

6. Ainu. The aborigines of northern Japan. Dark hair and eyes, excessive hairiness. Of the six white types, this is the only one which may represent a geographically isolated and thus a "pure" racial division.

The Negroid Race. Distinguishing characteristics of the Negroid race are black woolly or kinky hair, dark brown or black skin, black eyes, broad flaring nostrils, everted lips, protruding jaw, long forearm and lower leg, projecting heel, and underdeveloped calves. The Negroid race is divided into three main subraces.

1. African Negro. Typically as just described.

2. Nilotic Negro. Probably modified by the infusion of Mediterranean white blood. Distinguishing characteristics are reduced prognathism, narrower nose, less puffy lips, long slender build.

3. Negrito. Represented by the African and Philippine pygmies. Stature less than 4 feet

9 inches, woolly black hair, yellowish brown skin.

The Mongoloid Race. The Mongoloid is characterized by straight, coarse black hair, yellow or yellow-brown skin, often a fold of skin over the inner corner of the eyelid, fatty deposits about the eyes and cheeks. The Mongoloids tend to be short and stocky. The sub-races of this group are:

1. The classic Mongoloid as described above.

2. Arctic Mongoloid (Eskimoid). These differ from the classic type by having a broader face, more accentuated mongoloid jutting cheekbones, and a smaller fold of the eyelid.

Uncertain and Composite Races. In addition to the primary races, there are what appear to be intermediates and composites, perhaps products of the crossing of primary strains. Their classification is uncertain and few authorities reach agreement. Among these are the *Australoids*, *Polynesians*, *Melanesians*, *Indonesian-Malays*, American Indians or *Amerinds*, and the *Bushmen*. All these appear to be varying blends or offshoots of the basic Caucasoid, Negroid, and Mongoloid. Thus the Polynesians, light-brown skinned and smooth haired, are apparently a white stock thinly overlaid with Negroid and Mongoloid characteristics. It is curious that this triple blend has produced one of the most comely and physically perfect of racial types, such as the aboriginal Hawaiians. The woolly-haired black Melanesians, though variable, are distinctly Negroid. Australoids occupy a position somewhat between Caucasoid and Negroid, with peculiar features of their own, while the variable Amerinds show mixtures of components much like those found in the Polynesians, but with a much stronger infusion of Mongol. The small, yellow-skinned Bushmen of South Africa are thought to be offshoots of the Negritos, perhaps a mixture of pygmy Negrito with some Mongoloid features. How and when such a crossing could have occurred is one of the most puzzling of anthropological mysteries. Or perhaps this is an example of similarity due to parallel mutations.

Within each subrace there are subvarieties,

all of which mingle with each other. Thus the whole complex of racial variation is extremely tangled and promises to become even more so with the continued disappearance or weakening of geographical boundaries and barriers. It is impossible to predict what such trends will eventually produce, though it does not appear likely that it will be a uniform world race. It is perhaps more likely that the world population will eventually be a potpourri of all possible racial mixtures, and that parents of predominantly caucasoid cast, for example, would accept with equanimity a child of mongoloid or negroid type, just as brown-eyed, brown-haired parents today do not find it objectionable if their child turns out to be red-haired and blue-eyed.

Man appeared on the scene of life as *Pithecanthropus erectus*, already a user of tools. His relative, *Sinanthropus*, knew the use of fire. He was a cannibal, if we may judge by remnants of cracked human bones, and oddly shaped stones found with his bones may have been chipped stone implements of a simple style but "by no means the crudest known." After this auspicious beginning, with a command of fire and tools, we might well have cause to expect a swifter advance, but for the next four or five hundred thousand years, man appears to have changed culturally but little. His anatomy improved more than his skills and his tools — at least so far as we know. Each succeeding generation slavishly copied its craft from the preceding one, and original contributions must

have been rare indeed. Not until the last glacial period is there any marked improvement in the design of implements, and not until the Neolithic or new stone age is there any indication of the basic arts of agriculture, the domestication of animals, and the tedious and precise art of grinding and polishing stone tools instead of chipping them. It is almost unbelievable that the first knowledge of metal smelting, of writing, and of the use of the wheel dates back a mere five or six thousand years. Man's ability to control his environment is of extremely recent origin, only in its infancy, so to speak, for it has developed within less than one per cent of his time as man.

But his knowledge and his consequent mastery over matter and energy have begun to increase with terrifying speed — for with man there has appeared a radically new mode of evolution: social or non-genic inheritance, which has been made possible by the evolution of his cerebral cortex. Strip a modern man of his social heritage — his acquired knowledge — and he would be at once thrust back into the darkest regions of the Pleistocene. For with speech and writing came conceptual thought, whereby each man today incorporates within himself not only his personal experience, but that of countless thousands of others. Each modern man is a super-individual, and grafted upon his physically limited body is knowledge and experience that extends backwards even beyond the beginning of life and forward and outward indefinitely into time and space.

Man, the Supreme Mammal

This, then, is man, who out of the twilight aeons has in a few brief thousand years made such use of his fortunate physical endowments that he has become the dominant creature on the planet as no predecessor has ever done. Together his hand, his brain, and his speech have given him power over his environment and knowledge of it which no creature has ever approached. And all this has been done with a physical mechanism which is makeshift and imperfect at best — a skeleton which is typically mammalian except that it has been wrenched into an upright position; a nervous system essentially much like that of a cat except for the extraordinary development of the brain; endocrines not much different from those of most other vertebrates except for a few significant refinements; more or less typical mammalian sense organs, and muscular and reproductive systems that differ little from those of the higher mammals.

THE HUMAN FRAMEWORK

One of the most obvious differences between man and most of the higher vertebrates is a radical change in the principle of skeletal support, which yet came about with surprisingly little change in the parts of the framework. The skeleton of man corresponds almost bone for bone with that of the cat. But in all land vertebrates except the very lowest, the spine is a kind of bridge resting on two pairs of supporting columns. In man, however, this bridge-like structure has been radically altered by being up-ended for bipedal locomotion. If a large suspension bridge were stood on end to serve as a tower, certain fundamental changes would clearly be necessary. Such changes have taken place in the skeleton of man, notably

in the spine and the pelvis, thus fairly well but not completely adapting it to upright posture.

The Axial Skeleton

The Vertebral Column. The vertebral column, the skull, and the ribs comprise what is known as the axial skeleton. More than any other structure save perhaps the pelvis, the spine has had to undergo special modifications to meet the demands of upright posture (Fig. 454). Composed of thirty-three articulated vertebrae, it is the bridging span which has been stood on end. Compared with that of a typical quadruped the human spine is striking for its sinuous curves. Where in the cat a single arch sweeps from shoulder to tail, in man there is a marked reverse curve in the lumbar region as though the column had been bent back to achieve the erect body axis. Actually, this curvature softens shock, somewhat like a coiled spring, as it spreads the impact over a greater span of time. Interestingly enough, the spine is almost straight in an infant, and the curves develop and become functional as the child grows. Since bone formation is in part a function of external stresses, excessive or abnormal lateral curvature due to habits causing an uneven distribution of weight, habits such as carrying books in one arm, or habitually standing on one foot, may produce a permanent deformation.

In most higher vertebrates there is no great difference in the size of the vertebrae from pelvis to neck, but in man the lower vertebrae are larger and stronger. Automatic safety stops, the articular processes, prevent excessive movement of the vertebrae (Fig. 455), an important feature, since the spinal cord runs the whole length of the column, and the spinal nerves emerge through lateral spaces between

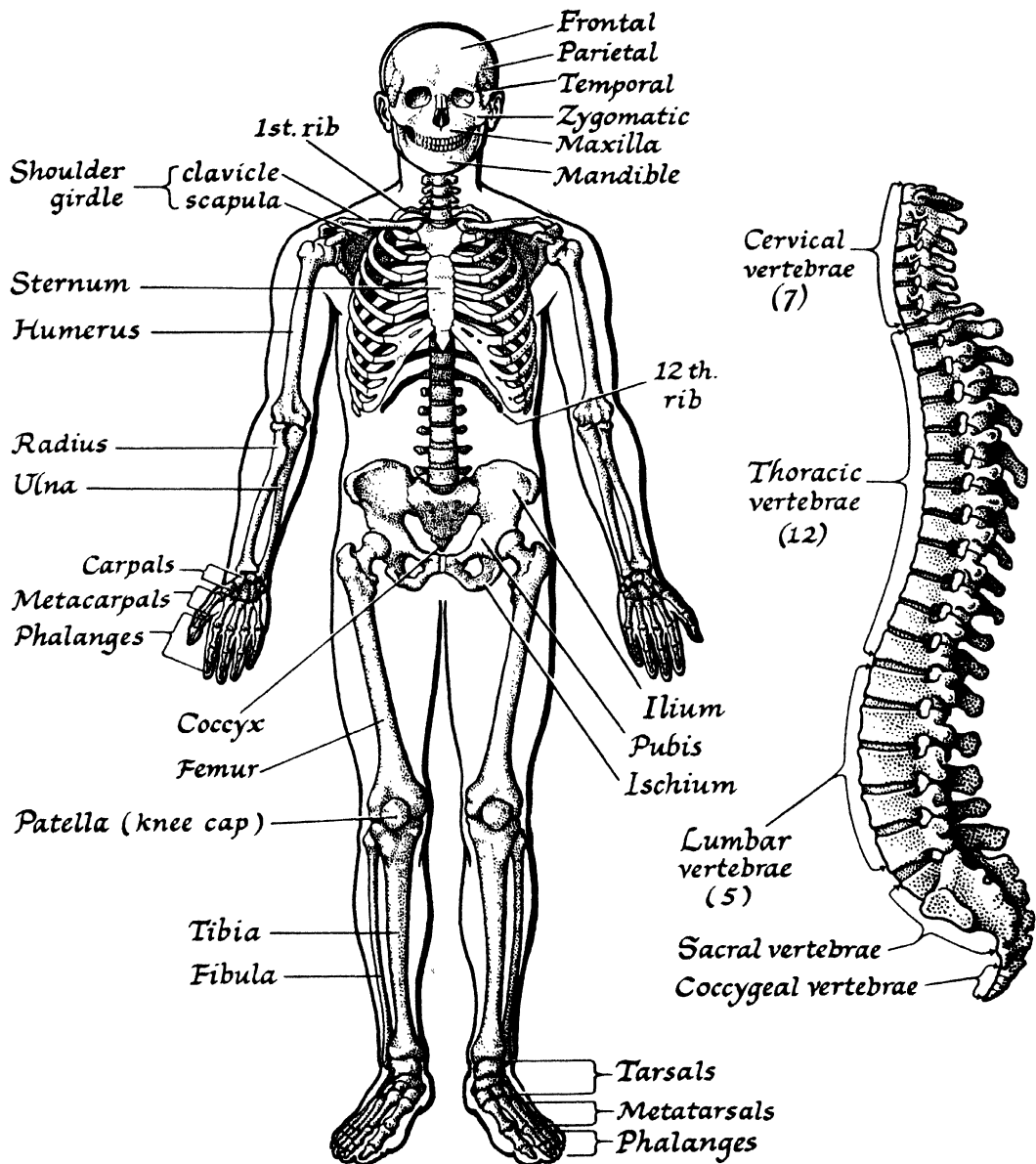


Fig. 454. The human skeleton (front view) and the vertebral column viewed from the left side.

the vertebrae. Different regions vary in amount of movement, and together they provide a fine range of flexibility. The whole string of vertebrae is so firmly held together that injury to the delicate cord is rare.

The column is attached to the *ileum* of the pelvic girdle by the five fused sacral vertebrae, thus forming the sacro-iliac joint (Fig. 454). This is perhaps the weakest feature of the axial skeleton, for the entire load must be held by the sacro-iliac ligaments, since there is no real

fusion of the bones at this joint. Frequently these ligaments prove unequal to the strain. They weaken, and displacement of the bones brings a host of pains and weaknesses.

The Skull. Much less specifically adapted than either man's spine or his pelvis is his skull (Fig. 456), which is much like that of most higher mammals except for a shift in emphasis from face to cranium and a change in position. The head of man rests on the vertebrae like a ball on a pedestal, whereas in the typical quad-

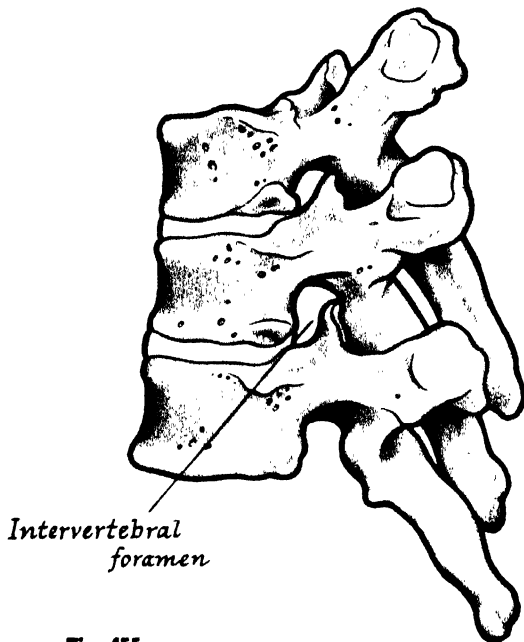


Fig. 455. Three thoracic vertebrae, showing their articulation and relationship.

rupted the head thrusts forward from the neck. The skull is still composed of twenty-two fused and sutured bones, exclusive of the six small bones of the ear and the U-shaped hyoid bone under the tongue.

Man is indeed in some ways less well off than his ancestors, for certain vestigial structures have become actual hazards. Among these are five sinuses (Fig. 457), air spaces lined with mucous membrane and perhaps once associated with the sense of smell in some keen-scented ancestor. The two *frontal* sinuses are located just above the eyebrows. Two more, the *maxillary* sinuses, are just below and towards the midline from the cheek-bones, and one, the *sphenoid* sinus, lies just below the base of the brain behind the nose. Since the sinuses are connected with the nasal cavity by ducts, and since these ducts in man run generally upward, instead of draining down as in four-footed animals, infections can easily spread from nose to sinus and lodge there, causing the all too well known sinus complaints.

The mastoid process is another danger point. This bony protuberance just behind the ear opening is filled with tiny air-spaces similar to

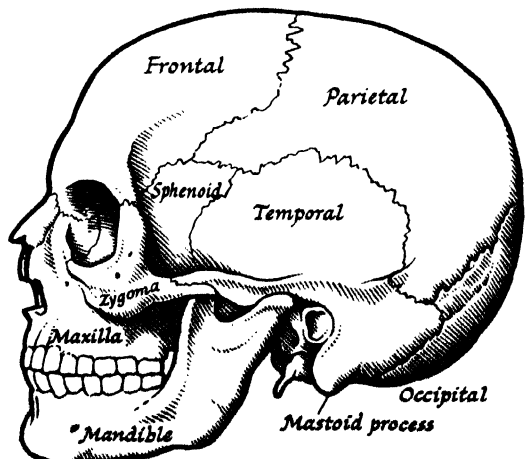
sinuses, and only thin bony partitions separate these from the middle ear and the brain cavity, thus facilitating a spread of infection from the nose (through the Eustachian tube to the middle ear) via the mastoid cells to the brain case.

Only three openings lead into the cranial cavity, one from each eye for the passage of the optic nerve, and a large one at the base for the spinal cord. Specifically human are (1) the greatly distended cranial cavity which houses the enlarged brain, (2) the shift of the opening for the spinal cord from the rear to the base of the skull, (3) the reduction in the size of the jaw and hence of the face, and (4) the shifting of the eyes from the side of the head to the front.

The Appendicular Skeleton

Shoulder Girdle and Forelimbs. The pectoral or shoulder girdle, which consists of two shoulder blades (*scapulas*) and two collar bones (*clavicles*), was modified by the brachiation of man's early ancestors. In contrast to most quadrupeds, the clavicle provides a more rigid foundation for the scapula, which is in turn an anchorage for the forelimb. Thus scapula and clavicle together form a triangularly braced girdle, capable of considerable free motion, yet reasonably rigid (Fig. 454). The scapula is attached to the rib case only by numerous sheets of muscles and can slide and rotate to a remarkable degree. Rare individuals born without clavicles demonstrate the bracing effect of

Fig. 456. The adult human skull. Note sutures of cranial bones.



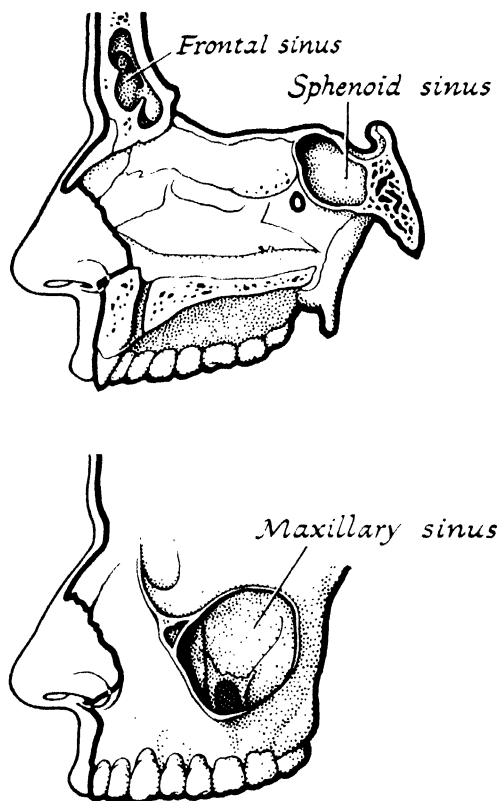


Fig. 457. Diagram of a section of the human skull showing frontal, sphenoid, and maxillary sinuses.

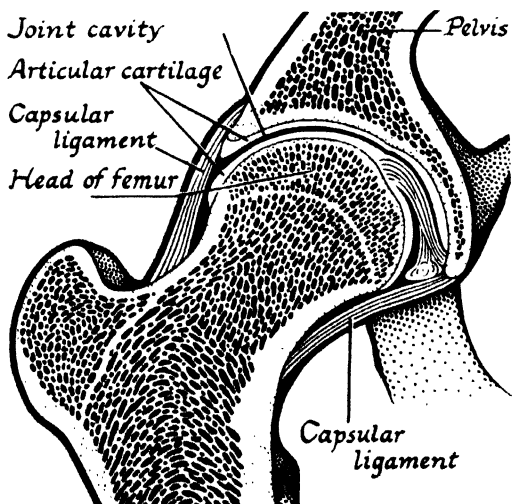
these bones, for such persons can bring their shoulders forward until they meet.

The ball and socket joint between the humerus, the bone of the upper arm, and the scapula, allows movement of the arm in any direction as well as rotation of it. The ulna of the forearm forms a hinge joint with the lower end of the humerus while its parallel neighbor, the radius, forms a flat articulation with the humerus. At the wrist, the ulna ends in a disk-like rotating head, while the radius flares out to form a wide hinge joint with the wrist bones (Fig. 454). This excellent arrangement allows the hand to make twisting movements, as in manipulating a screwdriver, and gives the wrist the flexibility of a universal joint. Gen-

erally not highly specialized, the human hand is rather typically and primitively vertebrate with the exception of the strongly opposable thumb. Its remarkable versatility comes not so much from its skeletal structure as from its muscles and nerves, which make it an exceedingly delicate tool.

Pelvic Girdle and Hind Limbs. From the long, narrow, and fragile structure found in the typical quadruped, the pelvis has been transformed in man into a wide, heavy basin supporting the abdominal viscera as well as transmitting weight from the spine to the legs. The girdle consists of two halves, each of three fused bones, the widely flared *ileum*, the *ischium* which forms the sitting base, and the *pubis*, which closes the girdle in front. The sacrum, consisting of five fused vertebrae, completes the girdle at the rear. On either side there is a deep cup into which fits the head of the *femur* or upper thigh-bone, forming the finest ball-and-socket joint of the skeleton (Fig. 458). Internally, the pelvis is open, and through the opening pass the digestive and urogenital orifices. It is also through this opening that the fetus passes in childbirth. Inevitably this brings about differences between male and female, the most conspicuous of which are the wider pelvic opening and the narrower point of fusion in the pubic bones of the female. Insuffi-

Fig. 458. Diagram of the structure of the hip joint. Note head of the femur inserted into the socket of the pelvic girdle. Note also the capsular ligament and the cushioning cartilage.



cient size of the pelvic aperture makes normal childbirth impossible, and requires removal of the fetus by incision through the abdominal wall and uterus in the Caesarean operation. The greater breadth in the female may cause a greater shift of weight in walking, so contributing to the more pronounced swaying of the characteristic female gait.

The femur — the longest bone in the body — is characterized by the pronounced ball at its upper end. At its lower end, it forms a broad hinge with the *tibia* or shinbone. The small outer bone, the *fibula*, helps to produce a recessed hinge joint for the articulation of the large ankle bone. One other ankle bone is especially large and forms the heel. *Metatarsals* form the main part of the foot, and the toes are degenerate. Two arches, transverse and longitudinal, give the foot a considerable degree of elasticity for shock absorption, more important in bipedal man than in quadrupeds. Stretched ligaments maintain these arches somewhat as a bowstring bends a bow. Hereditary weakness or abuse of the feet may break them down, producing flat-feet. Bone and nerve displacements in flat feet or fallen arches may markedly interfere with efficiency and may cause considerable pain.

The Bones as Levers

The bones and articulations form an intricate set of levers by which muscles produce movement. To appreciate the stresses to which our bodies are subjected, we should recall the principle of levers. It may be remembered that the product of a weight and its distance from a fulcrum on one end of a balanced lever exactly equals the product of weight and distance on the other. Thus a three-pound weight on a lever two feet long will balance a six-pound weight one foot from the fulcrum (Fig. 459). Applying this principle, it is clear that if a 150-pound man stands on the ball of one foot, the Achilles tendon pulling up on his heel bone will exert a pull of 392 pounds. If he leaps up into the air and comes down again on the ball of one foot, the strain will momentarily mount to five or six times the static figure, or to about

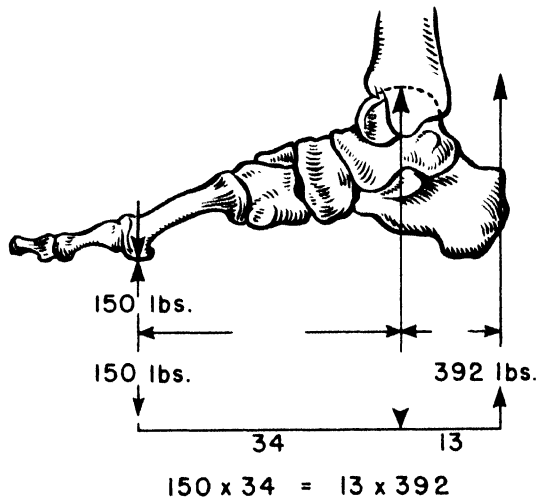


Fig. 459. Stresses on parts of the foot and its ligaments may be obtained by considering it as a simple lever. Here it is considered that the relative distance from the ball of the foot to the articulation with the tibia is 34 units as compared to 13 for the distance from the tibia to the heel tendon.

2000 pounds. The bony levers in our bodies are constantly being subjected to considerable strain.

THE SKELETAL MUSCLES

The bony system of levers in man is activated by over 400 muscles,¹ each a unit motor of contractile tissue, with a connective framework, nervous connections, and blood-vascular and lymphatic circulation (Fig. 460). These muscle units do not operate singly but are parts of a complex coordinated whole. Muscles are attached to bones by connective tissue either in flat sheets, called *aponeuroses*, or in rope-like tendons. It is customary to refer to one attachment of a muscle as its origin and the other as its insertion, the former being the relatively immobile end. In some muscles, however, this distinction may not hold. Thus the trapezius, a kite-shaped muscle in the back, may tilt the head back if the shoulder blade to which it is attached is held rigid, or may draw the shoulder blade up if the head is held rigid.

¹ For general discussion of muscles, see Chapter 18, pages 396-399.

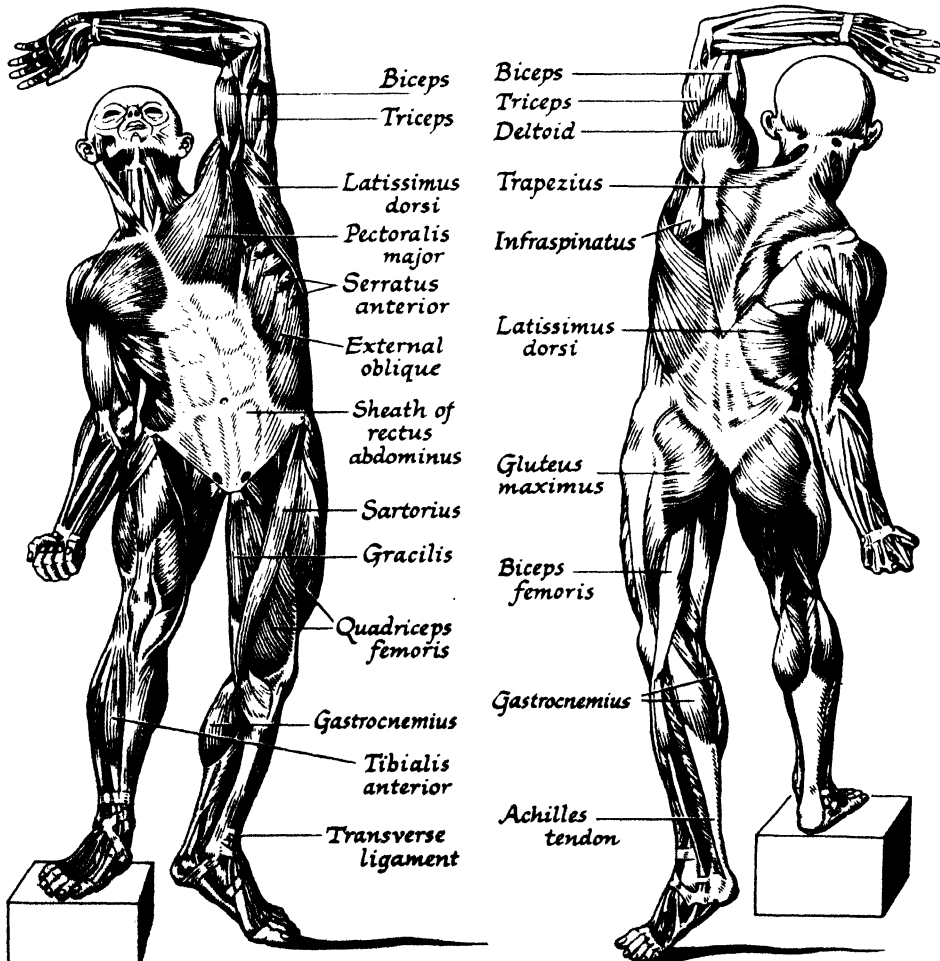
Muscle Coordination

Alone or in coordination, muscles perform a great many different types of motion. Some, like the triceps of the arm, may extend or straighten a part, or like the biceps, may flex or bend it. Others may pull a lever away from the mid-line of the body, as does the deltoid muscle, which caps the outer angle of the shoulder; or, like the fan-shaped breast muscle, the latissimus dorsi, may help to pull the lever back toward the body. Or a muscle may rotate a bone or limb about its own axis, as do the pectoralis major and the large latissimus dorsi, which latter passes from the lumbar vertebrae and up under the arm pit. The same muscle, of course, may do different kinds of work under

different conditions. Thus the deltoid may either flex or extend the arm or raise it away from the body.

Seldom does a single muscle work alone. Even the simplest activities call into action an astonishing number of different muscles, which are coordinated with consummate accuracy. Striking a blow, as with a hammer, involves the use of all the muscles of arm, shoulder, and thorax mentioned above, together with many more. Large muscles of back and chest give the main striking force, but the many muscles attached to the scapula must contract at the right instant to the proper degree in order to hold the point of insertion of the humerus steady in position. The muscles of the back

Fig. 460. The muscles of the human body, anterior and posterior views.



and abdomen must keep the spine erect upon the pelvis throughout the changing forces upon it during the action. The muscles of the forearm must flex the fingers around the handle; and even the muscles of the legs must cooperate as the center of gravity shifts, or the striker will lose his balance. In more complex actions like running, skating, or swimming, a correspondingly greater number of muscles becomes involved.

FOOD AND DIGESTION

Like his bones and his muscles, man's digestive organs are highly complex and specialized. Indeed, each section of the digestive tract performs one or more special digestive functions, aided by numerous groups of glands outside of as well as within the tract, each of which produces certain special enzymes which aid in the appropriate stages of the process.

Digestion begins in the mouth, where three pairs of salivary glands pour their secretion over the food as it is being ground, so that it is not only moistened and lubricated with mucus but its starch content begins to be hydrolyzed by a salivary enzyme, ptyalin. Then in the stomach the enzyme pepsin, working in the acid also present in gastric juice, begins to hydrolyze proteins, and the muscular movements of the stomach churn and further soften the food. In the small intestine still other enzymes, produced by the pancreas, attack all three food classes, fats as well as proteins and starches, and at the same time an intestinal secretion known as erepsin transforms protein fragments into amino acids while three sugar-splitting enzymes act upon the disaccharides (double sugars). While this is going on, bile juices, produced by the liver and previously stored in the gall bladder, assist in emulsifying fats. In the small intestine the process is practically completed, and the large intestine or colon secretes no enzymes, although those still mixed with the food continue their action. Absorption takes place mainly in the small intestine, which is lined by thousands of villi. Through the walls of these villi, substances pass into the elaborate capillary network in their interior.

The process of absorption continues in the large intestine, however, and here a large percentage of the water, as well as the remaining hydrolyzed substances, is absorbed.

One striking evidence of the imperfect adaptation of the human digestive tract is the presence of bacteria in both small and large intestines. Through their metabolic activities, these organisms frequently produce substances more or less poisonous, though the body usually converts or destroys them, furnishing an outstanding example of adaptability and of the power of selection in shaping organisms to their environment. In the small intestine, bacterial action is largely confined to carbohydrates, and the end products, lactic acid, acetic acid, and so on, are not markedly toxic. But in the large intestine, with most carbohydrates removed, the intestinal flora attacks proteins and protein fragments, causing putrefaction. Some are quite completely reduced, not only to amino acids, but these may be oxidized to produce such substances as carbon dioxide, ammonia, phenol, and skatol. Some of these are eliminated with the feces, but others are absorbed into the blood stream, where they may cause disturbances of the body metabolism and general discomfort. Although the intestinal flora appear to be of definite value in herbivorous animals, their value in man is not fully established. There is some evidence that they provide us with certain vitamins otherwise lacking in our food. Perhaps they may be considered as merely tolerated. Experiments now under way on animals raised from birth in an entirely germ-free environment may yield important information.

The Chemistry of Digestion

Although digestive glands secrete continuously, the nature and quantity of their secretions is coordinated with the food ingested. The salivary glands constantly moisten and lubricate the mouth, but stimulation of taste buds on the tongue sets off a reflex which increases their secretion many fold. Taste bud stimulus may also be substituted by a conditioned reflex of sight, sound, or smell. Approxi-

mately a quart and a half of saliva is produced per day.

Secretion of gastric juice creates its own problems, for the juice contains corrosive and proteolytic substances capable of digesting the stomach wall itself. It appears that the stomach saves itself from this fate only through its own constant activity. Pepsin reacts only in the presence of acid. The hydrochloric acid of the gastric juice is not produced inside the cells, but outside, in the cavity of the stomach, where chlorides from the blood stream are met by hydrogen ions released from the gland cells. In addition, the gastric glands produce a constantly renewed "varnish" of mucus, which covers the stomach wall. Failure of some part of this mechanism may result in stomach ulcers.

Gastric secretion is under the control of the nervous as well as the endocrine system. Though continuous, the flow of digestive juice increases when the gastric gland cells are stimulated through the nervous system. After the food enters the stomach, awareness of it fades, and further secretion is maintained by the action of gastrin, a hormone produced by endocrine glands within the stomach lining.

Pancreatic secretion, like that of the stomach, is under nervous and endocrine control. The proteolytic enzyme, here trypsin, is secreted as a precursor substance, trypsinogen. This becomes activated by a co-enzyme produced in the mucous membrane of the small intestine under the stimulus of ingested food. Here is also produced a hormone which acts upon the gall bladder.

Carbohydrate Digestion

Of the starches and sugars, the primary sources of energy, the monosaccharides or simple sugars ($C_6H_{12}O_6$) are readily absorbed through the body tissues and require no digestion. These are found as glucose and fructose in fruit. Disaccharides, such as cane sugar or sucrose ($C_{12}H_{22}O_{11}$), which are soluble but not readily absorbed, are split by the enzyme sucrose to yield the monosaccharides. Polysaccharides ($C_6H_{10}O_5$)_n, such as starch, must be

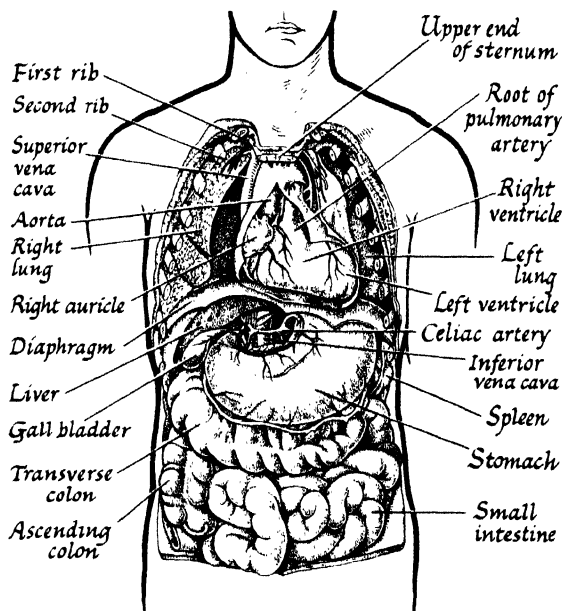


Fig. 461. The viscera of the human body.

hydrolyzed into monosaccharides. The enzyme in the saliva initiates the hydrolysis of starch into glucose. Further hydrolysis of polysaccharides does not occur until the food reaches the intestine. Here an enzyme similar in effect, but produced by the pancreas, takes over. Finally the disaccharides, sucrose (cane sugar), lactose (milk sugar), and maltose (malt sugar) are hydrolyzed to monosaccharides, each by a separate enzyme produced by the glandular cells of the small intestine.

Fats

The fats found in foods are generally mixtures of simple fats like palmitin, stearin, and so on. It will be recalled that the fat molecule is composed of one glycerol molecule to which are attached, by dehydration synthesis, three molecules of fatty acid. Digestion consists of splitting the fat molecule into fatty acids and glycerol again. The only enzyme able to do this is the lipase secreted in the pancreatic juice. Some of the fatty acids thus formed are

saponified by means of the bile salts present, thus sponsoring the emulsification of the remaining fat and maintaining it in the form of fine droplets with greatly increased exposed surface for rapid chemical action. Fat-soluble vitamins, such as vitamin K, cannot be absorbed from the food without this aid from the bile. The fatty acids and glycerol are absorbed through the villi within which, by processes not well understood, they recombine to form fats which pass on into the hollow core of the villus, starting point of the lymphatic system. From here they eventually find their way into the blood vascular system to be carried to fat deposits or to other tissues for consumption.

Proteins

Since man, and most other animals, can only synthesize about half of the thirty-odd known amino acids of which proteins are composed, he must obtain the rest already synthesized in his food.¹ Furthermore, since many proteins contain only some of the essential amino acids, it is evident that proteins must either be chosen very carefully, or a wide variety of them must be provided in the food as a safety factor. It is for this reason that milk is a valuable food, since it contains at least seventeen different amino acids.

Protein digestion is initiated by the activity of the gastric enzyme pepsin, which splits the complex and often insoluble proteins into simpler soluble ones. The soluble milk protein, caseinogen, however, is first converted into insoluble casein, in the form of curds, through the action of rennin. This delays its passage through the stomach sufficiently so that it may become hydrolyzed by pepsin. Were it to remain in its original liquid form, it would pass out of the stomach again in a matter of minutes, as does water.

Trypsin, an enzyme of the pancreatic juice acting in the small intestine, also reduces the complex proteins into shorter and simpler chains of amino acids, and finally the erepsin of

the intestinal secretion hydrolyzes these to single amino acid molecules, which are soon absorbed into the capillary network of the villi.

Mineral Elements

In addition to the organic components of food, certain minerals are essential to normal body metabolism. Outstanding among these are calcium, phosphorus, iron, iodine, sodium, potassium, magnesium, and chlorine. A normal, balanced diet, containing leafy vegetables, milk, eggs, and meat, is certain to contain a sufficient quantity of all these. Necessary to normal cell metabolism, they also play special roles. Calcium is essential for bone building and for maintaining normal muscular contraction and functioning of the heart. Iodine is essential to the production of the hormone made by the thyroid gland. Iron is needed for the synthesis of hemoglobin, and phosphorus is important in the chemistry of respiration.

Vitamins

Vitamins are a miscellaneous assortment of organic food compounds that perform various functions essential to life. How they do so is often as yet poorly understood. Some combine with proteins to make enzymes essential in tissue respiration. In general, however, the vitamins are better known for the deficiency diseases brought about by their absence than for the normal functions they perform. We saw in Chapter 4 that some of them play an important part in cell metabolism.

The table on the opposite page lists some of the main vitamins, their structure, deficiency symptoms, the effects of optimum intake, and their principal sources. The table is by no means complete.

The Liver

Perhaps the most important single organ in the entire digestive system is the liver, which is both a storage place for necessary substances such as sugar and vitamins, and also a chemical laboratory for the conversion of glucose into glycogen and back again, for the formation of

¹ For a discussion of proteins and amino acids, see pages 66-67.

bile, for the transformation of excess amino acids and complex fats into more usable fuels, and for the neutralization of toxic bacterial substances. The largest organ in the body, the liver fits snugly under the diaphragm.

Soluble foods and other compounds absorbed from the small intestine into the blood stream flow into the liver through the hepatic portal vein, while an hepatic artery supplies a small amount of freshly oxygenated blood. Branches

VITAMIN	DEFICIENCY SYMPTOMS	EFFECT OF OPTIMUM SUPPLY	SOURCES
A $C_{20}H_{30}O$ Provitamin-A-carotene Fat soluble	Retarded growth; xerophthalmia (dry eyes); night blindness; dry skin; inflammation and infection of alimentary tract	Resistance to skin infection; general health and vigor; normal vision	Fish liver oils and animal livers ~~Egg yolk~~ Green vegetables Butter Yellow squash, sweet potatoes, ~~carrots~~
B₁ $C_{12}H_{16}N_4SO$ Thiamin Water soluble	Beri-beri or polyneuritis; stunted growth; loss of appetite	Normal carbohydrate metabolism; normal appetite and digestion	Yeast Whole grain Vegetables Fruit juice
B₂ (G) $C_{17}H_{20}N_4O_6$ Riboflavin Water soluble	Cataract; skin defects around mouth and ears; metabolic disturbances, retarded growth	Normal growth and nutrition	Yeast Egg white Green vegetables Liver
P-P Niacin $C_{28}H_{44}O$ Water soluble	Pellagra; skin and spine disturbance; digestive disturbance	Normal digestion and normal skin	Yeast Glandular organs Vegetables
C $C_6H_8O_6$ Ascorbic acid Water soluble	Scurvy; retarded growth; dental caries	Normal teeth; healing of wounds; protection against infection	Citrus fruit Tomatoes, and other fruit
D $C_{28}H_{44}O$ Calciferol Fat soluble	Rickets in children; defective bones and teeth; retarded growth	Normal bone growth	Animal fats Fish liver oils Milk Egg yolk Oysters
E α -tocopherol $C_{29}H_{50}O_2$ Fat soluble	Sterility in rats and possibly in other organisms; also paralysis	Normal fertility in rats	Wheat germ oil Meat Egg yolk
K $C_{31}H_{46}O_2$ Fat soluble	Delayed clotting time in blood, hence excessive bleeding	Normal blood clotting	Leafy vegetables Liver
B₇ Folic acid	Macrocytic anemia; sprue?	Normal growth	Spinach Yeast Kidney

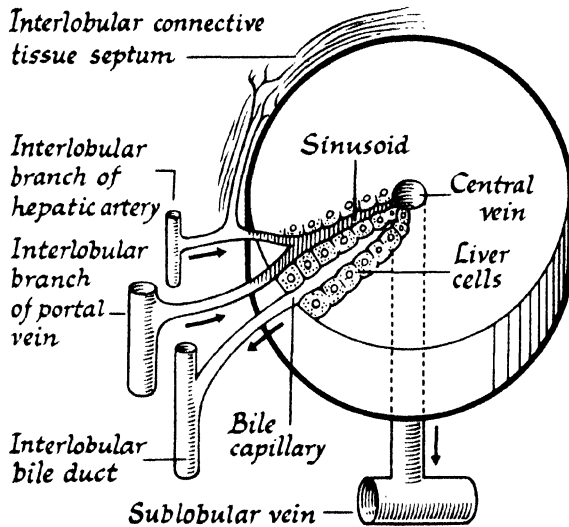


Fig. 462. Diagram of a liver lobule showing the course of circulation.

of the portal vein radiate toward the core of each of the many lobes of the liver by means of incompletely enclosed sinusoid vessels, so that the blood comes into direct contact with the liver cells (Fig. 462). Here the liver performs its chemical work on the constituents of the blood, which is then collected again into veins that join to form the hepatic veins leading toward the heart. Also leading out of the liver are bile ducts, which carry the secretions and excretions of the liver into the gall bladder.

The secretion of the liver, bile, contains substances synthesized in the liver and not found in the blood. While it is largely a waste product made up of decomposition materials resulting from the destruction of red blood cells, bile also contains bile salts, that is, salts of bile acids, substances related to amino acids in structure. These salts have numerous functions, among them being the emulsification of fats, the activation of lipase from the pancreas, and the maintenance in soluble form of cholesterol. They are necessary for the absorption by the intestine of vitamins D, E, and K, and of carotene (pro-vitamin A). The bile salts are reabsorbed in the small intestine and delivered back to the liver where they are used over again.

The liver is no less important in controlling the nature and quantity of dissolved food-stuffs in the blood. A high concentration of glucose flows into the liver after each meal. By an enzyme, all above the quantity required to replace current consumption by the cells of the body is transformed into the insoluble animal starch, glycogen. Thus the blood-sugar level remains constant even after meals, with the liver acting as a depository for the transformed glucose. As metabolism removes soluble sugar from the blood, the same enzyme reverses the reaction and almost instantaneously transforms stored glycogen again into glucose, thus maintaining the stability of the blood-sugar concentration.

Still another function of the liver is that it selectively deaminates amino acids and transfers their nitrogenous fragments (NH_3 , ammonia) to the amino acid arginine, which promptly decomposes to form another amino acid, ornithine, and urea. The remaining fragment of deaminated amino acid is converted into glucose, and may either be stored as glycogen or released into the blood stream.

Again, certain cells of the liver, called Kupffer cells, ingest fat globules and partially catabolize them into compounds more readily available for use by other tissue cells of the body. This is accomplished by a partial oxidation of fatty acids. Finally, the liver converts some of the absorbed toxic end products of intestinal bacterial action into non-toxic forms which may then be excreted by the kidneys. It is also able to lay aside stores of vitamins A, B_1 (thiamin), and D. The liver is a chemical laboratory which performs many functions.

THE CIRCULATORY SYSTEM

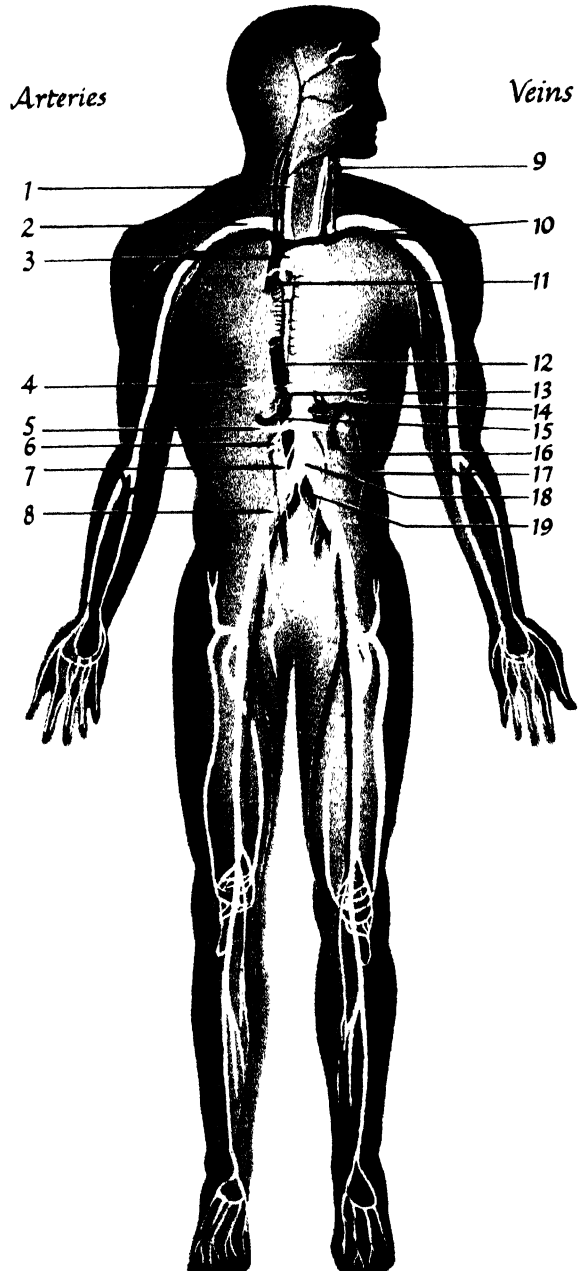
The Heart

The pattern of human circulation is essentially like that of every other mammal, and differences are surprisingly minor in character. There are two circuits, the pulmonary, which sends blood to the lungs and back to the heart again, and the systemic, which distributes it throughout the body (Fig. 463). The vital

center of the system is the typical four-chambered mammalian heart, which in man is about the size of a closed fist and shaped somewhat like an acorn tilted to one side. Actually it is little more than a highly specialized muscle, chambered and hollow, surrounded by a double sheath of protective tissue as though swathed in a partially inflated rubber balloon.

The familiar heart sounds — “lubb-dup, lubb-dup” — are caused by the shutting of the valves which prevent back-flow from the ventricles to the auricles and from the arteries back into the ventricles. The first dull boom is the slapping shut of the great sail-like flaps between the auricles and the ventricles, as the latter constrict and force the blood into the pulmonary artery leading to the lungs or into the aorta, the great artery feeding the entire systemic circuit. The second, sharper sound is the closing of the vest-pocket-shaped valves at the mouths of these vessels which, now filled with blood, begin their own contraction as the emptied ventricles relax (Fig. 464). By listening to these heart sounds, a physician can detect flaws in heart or blood vessel structure. These announce themselves by various “murmurs,” humming or gurgling sounds. Constriction of the aorta may cause one sound, leak in the auriculo-ventricular valves another. Ceaselessly beating from the time when it is no more than an S-shaped bent tube within the $3\frac{1}{2}$ weeks old embryo, then scarcely 2.5 mm. long, until death at old age, the heart does a prodigious amount of work. Beating at a steady rate of 70 per minute, there are over 100,000 beats in 24 hours, almost 40,000,000 in a single year. Knowing the pressure behind the blood pumped by the heart, and the quantity pumped out at each contraction, the energy expended in each contraction can be computed, and is found to be approximately two foot-pounds. This adds up to about 140 foot-pounds per minute, the equivalent of $\frac{1}{4}\frac{1}{10}$ horsepower (1 H.P. = 33,000 foot-pounds per minute). Were the heart energy concentrated on lifting a weight, it would be sufficient to lift the owner of the heart one foot off the ground every minute of the day, or to a total height of almost

Fig. 463. The human circulatory system. Arteries (white): 1. Common carotid. 2. Subclavian. 3. Aortic arch. 4. Coeliac. 5. Renal. 6. Superior mesenteric. 7. Genital. 8. Common iliac. Veins (black): 9. Internal jugular. 10. Subclavian. 11. Superior vena cava. 12. Inferior vena cava. 13. Hepatic. 14. Hepatic portal. 15. Renal. 16. Superior mesenteric. 17. Inferior mesenteric. 18. Genital. 19. Common iliac.



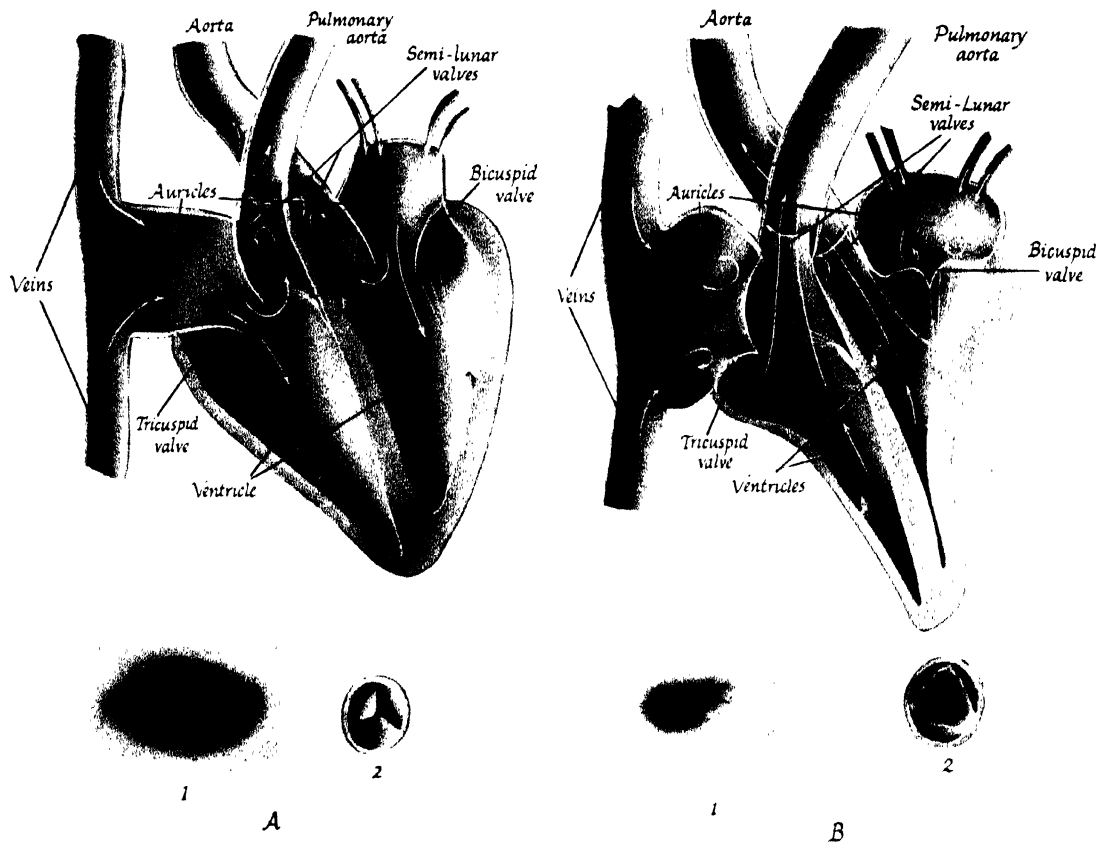


Fig. 464. Sequence of heart contractions. *A*. Diastolic phase. The contracting auricles push blood into the ventricles. Pressure in the veins has dropped and they have decreased in diameter. The semilunar valves are kept closed by blood pressure in the arteries, whose elasticity slowly squeezes the blood toward the capillaries. 1. Top view of bicuspid valve, open during this phase. 2. Closed semi-lunar valves. *B*. Systolic phase. The contracting ventricles push the blood through the now-open semi-lunar valves into the arteries. Pressure in the ventricles has closed the bicuspid valves. Blood from the veins accumulates in the auricles and distends the veins. 1. Bicuspid valve, closed. 2. Semi-lunar valve, open.

1500 feet in a single day. It is remarkable that such a small organ should be capable of yielding such uninterrupted power over the span of a lifetime.

How the Heart Beats. The heart acts as a single unit in beating, and its capacity to beat is autonomous, for pieces cut from heart tissue will continue to live and beat if properly nourished. The rate of the heartbeat is controlled by a knot of specialized muscular tissue. In mammals, this "pacemaker" is the *sino-auricular* (S-A), or simply *sinus node*, located near the terminus of the great veins in the wall of the right auricle. The contraction impulse swiftly spreads from here to all parts of the

auricle. In the dog, the entire auricle is excited within 30 to 45 milliseconds. Since auricles and ventricles are separated by relatively non-muscular tissue of less than normal conductivity, the contracting impulse is conducted to other parts of the heart from the *atrio-ventricular* (A-V) node by a narrow strand of muscular tissue called the *bundle of His*. Impulses starting in the auricle are thus swiftly imparted to the ventricles, but a "block" within the system prevents a reverse flow of impulses.

Two sets of motor nerves control the pace-making of the sinus node. The *vagus* nerve acts as an inhibitor, while numerous fibers of the sympathetic system act as accelerators. There

are also two sets of fibers leading from the heart to the *cardiac center* in the *medulla*, which is thus kept informed of conditions and demands in the heart. One set, called depressors, leads from the aortic arch and by reflex action through the vagus slows the heart beat whenever the pressure in the aorta rises; another set, the pressor fibers from the right auricle, work through the accelerator fibers to begin the new beat.

The Plan of Circulation

The basic improvement of the mammalian circulatory system over that of other vertebrates, excepting the birds, is the possession of two separate loops in series (see page 429). From the heavily muscled left ventricle, blood leaves for all parts of the body by the great aorta. Chance alone dictates which of the numerous possible paths any drop of blood may take, whether to brain, arms, stomach, kidneys, or legs. But sooner or later it passes through capillaries where it yields dissolved foods, oxygen, water, and salts; it may absorb carbon dioxide and nitrogenous wastes. If it happens to pass through the kidneys, it loses wastes, such as urea, but continues to absorb carbon dioxide. Thus a molecule of waste may circulate through the body many times before it finds its accidental way to the kidney. If the blood chances to be diverted to the intestines, it picks up foods and water, provided the digestive system is at the moment absorbing digested foods. Also, of course, as in all tissues, it accumulates CO₂ and other wastes. Thus changed in various ways, the blood pours back into the veins, all of which save the portal vein (pages 511-512) lead back to the heart.

The blood does not return to the left side of the heart but to the right, the beginning of the pulmonary circuit, leading to the lungs. Return of the blood through the pulmonary veins to the left auricle completes the pulmonary circuit and the whole cycle. This double system, found only in birds and mammals, while still not perfect, is vastly more efficient than the single circulatory system which is found in lower vertebrates.

The Blood Vessels

Blood vessels are complex, responsive organs. The larger ones are built up of three tissue layers, each with a lining of elastic connective tissue, a middle layer of elastic tissue and circular muscles, and an external layer of connective tissue and longitudinal muscles. This is true of both arteries and veins, but arteries, which have to withstand much greater pressure, have heavier walls. The thickness of the layers decreases in the smaller vessels, until the capillaries consist of but a single, porous layer of thin, flattened cells. The diameter of the vessels varies from 1½ inches (the aorta) to only 8 μ or less in the capillaries, which are just big enough for the blood cells to pass through. The extensiveness of the system is almost unimaginable. How densely the capillaries are packed in every organ and structure is evident from the fact that even a pin prick is likely to strike a blood vessel. It has been estimated that if all the vessels in a single human being were laid end to end, they would extend about twice around the earth!

Blood Pressure

As the blood is forced into the elastic arteries, the pressure within them rises. Then, while the heart rests between beats, the elastic pressure of the arteries forces the blood forward and smooths out the pulsing flow into a smooth and steady one. Thus the shock-wave set up by the violent contractions of the ventricles is gradually absorbed. Because of the loss of energy through friction as the blood flows through the thousands of miles of capillaries, the relatively high arterial pressure falls to a low point in the returning veins. That is why blood merely oozes out of a cut vein but spurts from an artery. Loss of arterial tone, which happens with the mineralization and loss of elasticity in arterial sclerosis, or "hardening of the arteries," may lead to serious consequences, among them, the rupturing of small blood vessels. If these are in the brain, the cerebral hemorrhage may cause paralysis and death.

A physician can draw valuable conclusions

about the condition of the heart and the blood vessels from measuring the blood pressure. What he measures is the pressure in the radial artery of the arm, both at the peak of pressure and at its low point. The instrument used for this purpose consists merely of a wide rubber tube to which is attached an inflating bulb and a pressure gauge. The tube is wrapped around the arm and inflated until only at peak pressure can a small spurt of blood force itself through the radial artery under the bandage. The pressure at this moment, as recorded by the gauge, is the peak or *systolic pressure*. As the pressure in the bandaging tube is further released, the artery, which closes after each pressure peak, finally reaches a point where it can remain open. The beating sound of its closure vanishes at this moment, and the pressure then recorded is the *diastolic pressure*. Thus the pressure effects of exercise, illness, valvular lesions, weight, sex, stature, and age can be determined. High blood pressure places an increased burden upon the heart. The seriousness of this is apparent from the fact that heart or some other circulatory failure is by far the principal cause of death in the population of the United States.

Control of Blood Flow

Increased or decreased activity of the heart of course influences the rate of blood flow, but this alone would not be adequate to meet the demands of different organs under varying conditions. During and after a meal, the viscera are especially active. In muscular activity the skeletal muscles require more blood. These demands are met by local dilation or constriction of blood vessels. The capillaries are under the direct chemical control of the carbon dioxide concentration in the blood flowing through them. The muscles of the arterioles (small arteries) are controlled by the nervous system. Among coordinating chemicals, carbon dioxide and adrenalin have pronounced effects. Active tissues produce an excess of carbon dioxide, which permeates the tissues around the capillaries and causes them to dilate. Injections of adrenalin cause dilation of the small arteries in

skeletal muscles, but constriction in those of the viscera. Perhaps normal secretion of this hormone, in crisis or alarm, is responsible for the rush of blood away from the digestive organs and into the muscles which takes place.

Nervous control of blood vessels is achieved by two sets of nerves, constrictors and dilators. The vaso-constrictor muscles are normally partly contracted and maintain a submaximum circulation. Cutting their nerves results in dilation of the affected blood vessels. Stimulation of the vaso-dilator nerves accomplishes the same result. The precise neuro-muscular mechanism is still obscure, but it is clear that these two systems between them closely control the supply of blood to every part of the body.

The Blood

Human blood is a viscous and rather sticky fluid, slightly heavier than water, and comprises almost one-twentieth of the body weight, or about five quarts for the average man. The blood is about 90 per cent water, which acts as a solvent, as a vehicle for the transportation of blood cells, nutrients, and wastes, and actually takes part in many chemical changes.

Blood Plasma. The liquid portion of the blood, known as the *plasma*, contains a number of things besides water. There are salts, both in the form of nutrients and wastes, and as regulators. Among other nutrients are amino acids, glucose, fatty acids, and glycerol, which are absorbed and assimilated or catabolized by all tissue cells. There are wastes — urea, uric acid, and many others — to be filtered and removed by the kidneys; blood proteins, which regulate the consistency, clotting, and osmotic pressure of the blood; other regulators such as hormones, vitamins, enzymes, and other special substances which act as coordinators and regulators of metabolism; and finally, there are antibodies, which weaken and destroy bacteria and neutralize the poisons they release. Indeed, the blood is one of the most complex parts of the human organism.

Blood Cells

In addition to the plasma there are two main types of blood cells, the red cells or *erythrocytes*,

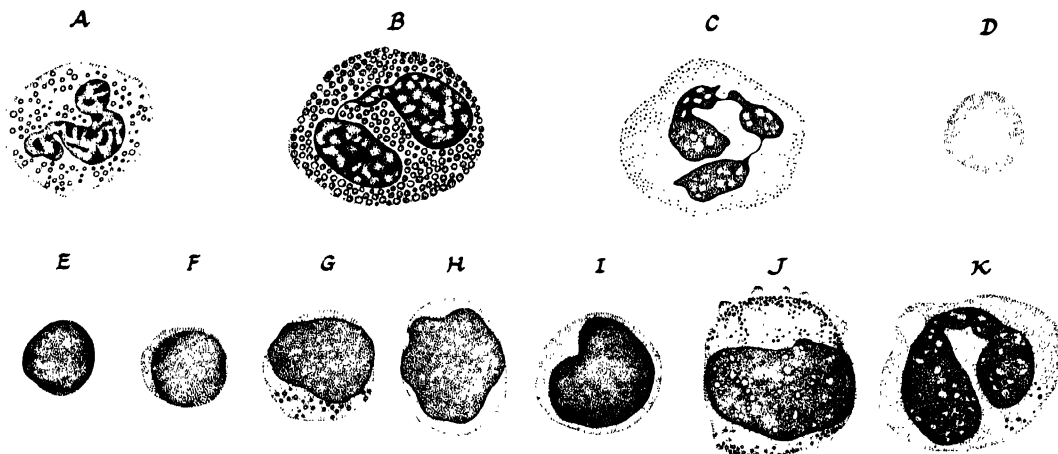


Fig. 465. Types of human blood cells. *A-C*, Polymorphonuclear leukocytes (basophil, eosinophil, neutrophil); these constitute 60 to 70 per cent of the white cells. They excel in amoeboid and phagocytic activities and are the primary policing force. *D-E*, Erythrocytes, the red, oxygen-carrying cells of the blood. *F-I*, Lymphocytes, mainly in lymphoid tissue, probably active in tissue repair. *J-K*, Monocytes, probably developed from lymphocytes.

and white cells of several varieties collectively called *leukocytes*. There are also the small blood platelets.

Red Cells. Of the various types these are by far the most numerous, there being about $4\frac{1}{2}$ million per cu. mm. in women and about 5 million in men. They are shaped like thick disks concave on both sides, such as might be formed by pinching the sides of a flat clay pellet between thumb and finger. Only $7.7\ \mu$ in diameter, their collective surface is amazingly large because of their immense numbers. It is estimated at about 3000 square meters, enough to cover the outer wall surface of six barns each measuring 40 by 50 feet and standing 25 feet high at the eaves. This great cell surface serves almost exclusively to carry oxygen in chemical combination for respiratory purposes.

Human red cells have a limited life-span, for they are cell fragments lacking a nucleus. Their average rate of replacement may be computed from the amount of hemoglobin liberated per day, about 25 grams. This is the amount normally present in 160 cc. of blood, or roughly one thirtieth of the total amount present in the body. From this we may conclude that the average life of a red blood cell is about thirty days, though many red cells live as long as fifty or even a hundred days. Even at this rate, approximately 10 million of them are normally removed from the blood each second by liver

and spleen — and of course, an equal number are produced in the red bone marrow.

White Cells. The leukocytes are present in a proportion of only about 1 to 700 red cells, 5000 to 9000 per cc. of blood, and they are far less homogeneous in type than the red cells. They range in size between $10\ \mu$ and $20\ \mu$ and are generally classified according to nuclear structure, reaction toward dyes, and visible cytoplasmic structure. Most of them — up to 60 per cent — have lobed nuclei and a somewhat granular cytoplasm; these, known as *neutrophils*, ingest bacteria or bits of decomposing cells and respond positively to a variety of chemical stimuli. Another type, the *lymphocytes*, may represent over 30 per cent of all white blood cells in the body. These, with a relatively large nucleus and non-granular cytoplasm, are relatively indifferent to chemical stimuli. Their function is not entirely clear, although their concentration at infected points suggests that they play a role in warding off infection. There is evidence that they are the producers of antibodies, along with similar but non-wandering cells in the numerous lymph glands and the spleen. They may also play a part in resisting cancer. Enzymes liberated by degenerating lymphocytes assist in liquefying dead tissue.

Especially large leukocytes, called *monocytes*, with a characteristically indented nucleus, com-

pose about 5 per cent of the white cells. These are unusually active in ingesting bacteria and cell fragments and appear to assist in tissue repair.

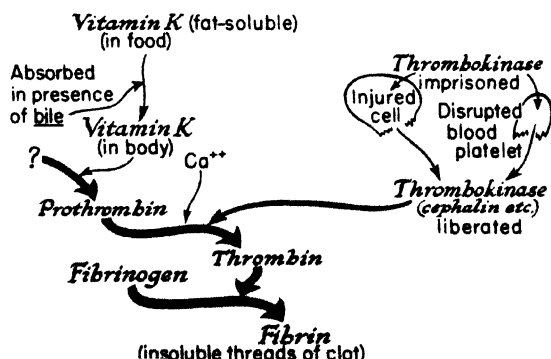
The rate of reproduction of leukocytes varies with the chemical composition of the blood. Local infections not only draw a swarm of neutrophils, but in a healthy body cause a marked general increase in the number of these cells. Thus a blood count, that is, a check on the relative number of different kinds of cells in the blood, informs the physician of possible hidden infections.

Blood Platelets. The last of the cellular components of the blood are the blood platelets. Measuring only 2 to 4 μ in diameter, these cell fragments are small compared to the 20 μ white cells or even the 7 μ red cells. Since there are about 300,000 platelets per cc. of blood, there are about 50 of them to each white cell. Their primary function appears to be in blood clotting, an extremely important phenomenon, since if it did not occur, any minor cut might mean death by hemorrhage.

Blood Clotting

Perhaps one of the most striking features of the circulation is the automatic ability to seal breaks anywhere in the system. Without some such provision the type of organism based upon a circulatory system would not have been capable of surviving. Those unfortunate individuals afflicted with a heritable disease known as *hemophilia* clearly verify this statement.

Fig. 466. Substances which take part in the mechanism of blood clotting. Question mark at left indicates unknown substance or substances which become a part of prothrombin. Note separate systems involved in production of thrombin.



"Bleeders," as they are called, have blood which will not clot rapidly, and the slightest scratch or internal break causes long-continued bleeding. Even with the aid of modern medicine, their life-span is short. In normal human beings, as in all mammals, the flow of blood from a broken vessel is stopped by an involved series of chemical changes in the blood, causing its solidification or clotting. There are differing theories as to the precise sequence of events causing this, but the process may be somewhat as indicated in Fig. 466. Normally present in the plasma are *prothrombin*, *thrombokinas* (or *cephalin*), and *calcium salts*. Under suitable conditions, these interact to form active *thrombin*. Under normal conditions the thrombokinas is imprisoned in living cells and in the blood platelets; but when tissues are injured or blood is exposed to the air, the thrombokinas is liberated and large quantities of thrombin are produced. This combines with the ever-present blood constituent fibrinogen to form the insoluble strings of fibrin which are the basis of the blood clot. Thus the ingredients which unite to form a blood clot are normally prevented from meeting, but when the first step is completed, all the others follow and clotting ensues.

Clotting normally occurs only when it is needed to prevent blood loss, but the mechanism can miscarry. Introduced, non-absorbed air, internal injury, linings of blood vessels roughened through disease, hindered blood flow — all of these may release the clotting sequence and so cause an internal clot. Should this become dislodged, it may cause swift death by plugging some vital artery, such as the coronary artery of the heart.

Blood may sometimes be prevented from clotting by avoiding the disruption of platelets or injury of tissues. Blood carefully drawn from an artery into a paraffined vessel will not clot. Hemophiliacs, strangely enough, fail to show a lack of any of the known substances necessary for clotting. However, their platelets appear to be unusually resistant to injury. The change from prothrombin to thrombin seems also to be retarded.

Blood Types

Just as individuals differ in hair color, eye color, skin texture, and innumerable other characteristics, so they differ in the chemical composition of their blood. Only a few of the possible differences in blood composition have been established, but these are of practical value in making successful transfusions, and through them racial as well as individual or family relationships may be established.

Briefly, specific genes, which play a dominant role in determining the production of certain blood chemicals, have undergone one or several mutations which in various combinations produce series of blood types. Three blood groups or series are now well known. They are the Landsteiner or ABO group, the MN group, and the Rh or Rhesus factor group. The one earliest known to be important in blood typing for transfusion is the ABO group, which may be used to illustrate the principle of typing.

Two sets of two characteristics are involved: (1) two substances in the red blood called agglutinogens A and B; and (2) two substances in the plasma called agglutinins α and β . Agglutinin α causes red cells with agglutigen A to agglutinate, or clump together. A similar relationship holds for β and B. Agglutinin and agglutigen of a pair therefore cannot be present together in the same individual. However, an individual lacking a given agglutigen for some reason always carries the corresponding agglutinin. Individuals completely lacking any agglutigen in their red cells consequently have both agglutinins α and β in their plasma. Those with A have β , those with α have B, and those with A and B have neither agglutinin α nor β .

The relationships between the four possible blood groups are shown in the table below.

Thus group O cannot have its cells agglu-

tinated by the plasma of any other group, since its cells contain no agglutinogens. However, in transfusions, the whole blood of one individual is introduced into that of another and the red cells of any other type introduced into a person of type O will be agglutinated. Donors for transfusions to type O individual should therefore also be type O. But, ironically, a type O individual may donate his blood to any other group, making him a universal donor. For if his blood is slowly introduced into that of another type, his agglutinins will be so diluted as to be harmless, and his cells, free of agglutinogens, cannot be clumped, anyway. But reverse the flow, and the agglutigen-bearing cells of A, B, or AB will find themselves in a concentrated solution of agglutinins α and β , and will clump. For similar reasons, group AB is a universal recipient, but quite unsafe as donor for persons of any other type. However, in emergencies, it is best for donor and recipient to be identical in blood type. Since the introduction of this classification, these groups have been found to fall into several sub-groups.

The Rh Factor. More recent is knowledge of the Rh or Rhesus factor, a blood cell antigen present in about 85 per cent of the white population, and first discovered in the Rhesus monkey. An individual without the Rhesus factor may develop antibodies to the Rh antigen if exposed to red cells carrying it, and these antibodies have a hemolytic action upon the Rh+ erythrocytes. In this, and in the fact that the Rh factor is heritable, lies its importance. An Rh- mother mated to an Rh+ father may conceive an Rh+ child. Under certain conditions, the Rh+ erythrocytes of the child may stimulate Rh antibodies in the blood of the mother. These may enter the circulatory system of the fetus, causing stillbirths, jaundice, anemia, or "erythroblastosis," as it is called.

LANDSTEINER GROUPS	AGGLUTINOGEN IN CELLS	AGGLUTININ IN PLASMA	PLASMA WILL AGGLUTINATE	CELLS WILL BE AGGLUTINATED BY
O	none	α and β	A, B, and AB	none
A	A	β	B and AB	O and B
B	B	α	A and AB	O and A
AB	AB	none	none	O, A, and B

Similarly, transfusions of Rh+ blood to a sensitized Rh- mother may produce damaging results in the mother.

ROLE OF THE BLOOD IN PROTECTION AGAINST DISEASE

The cells of man, like those of many metazoans live bathed in blood plasma, and their welfare is determined by its composition. Besides transporting nutrients and removing wastes, the blood transports and perhaps supplies many specific substances which enable the organism to survive in a world of ever-threatening microbes. Every surviving creature has been selected, through the ages, both for its ability to compete and survive, and to withstand attacks in turn. For every living creature there are hosts of predators and parasites whose existence depends on their ability to overcome the defenses of their potential host. In many cases selection has produced miracles of specialization in both camps, each becoming successful enough to maintain its species despite the best efforts of the other. In man, blood plays a vital role in this warfare, together with his other defenses.

From our knowledge of the blood and its ingredients, the symptoms of inflammation take on a new significance. Bacterial toxins paralyze and destroy the tissues, including the muscular fibers that normally constrict the capillaries. These then become enlarged and engorged with blood, causing local redness, swelling, local rise in temperature, and pain due to distention. White blood cells respond by penetrating the distended capillary walls and indulge in phagocytic orgies. They may emerge victorious and return into the circulatory system, or they may be overcome by bacterial toxins and disintegrate. Red blood cells too may leak out into the battlefield, adding to the litter of dead blood cells, bacteria, and destroyed tissue, forming a collection called pus. Usually the reserves of the body overcome the bacterial attack, and leukocytes may then contribute to the healing process, some of them actually becoming transformed into connective or scar tissue. If toxin forma-

tion and destruction proceeds at a greater rate than can be mastered, the destruction of tissue may become widespread, and the toxins then poured into the blood may eventually reach a level destructive to some vital organ, and result in death.

The Kinds of Organisms that Threaten Man

While man has successfully eliminated all of his larger potential enemies save his fellow man, invisible hosts of microorganisms remain. These include the filterable viruses, among them the agents causing smallpox, infantile paralysis, rabies, and yellow fever, as well as the common cold. There is also the immense variety of bacteria, the causes of common infections and of pneumonia, gonorrhea, diphtheria, tuberculosis, typhoid, plague, and hosts of other diseases. There are parasitic fungi, causing ringworm, athlete's foot, actinomycosis, and similar annoying and sometimes vicious skin irritations. And finally there are disease-producing protozoans, such as those responsible for syphilis, malaria, amebic dysentery, and a good many other ailments. The mere fact that most of these names are known and dreaded bespeaks the magnitude of their threat.

Channels of Infection

Usually man's living tissue is not openly exposed to the attack of microorganisms, and the blood, although of the utmost importance, is not the first line of defense. The complex skin is one of man's most stalwart defenses, for unless it is broken, most organisms find it impregnable. But a completely unbroken skin does not exist, and were this our only defense, we would not be long of this earth.

Because of the necessary thinness and delicacy of the tissues of the respiratory, digestive, and urogenital systems, these are relatively vulnerable, as are parts of the eye and the ear. Substances secreted by these various surfaces, such as acids, salt solutions, and fats, often successfully balk the entrance of microorganisms. But sooner or later every one of these defenses must yield, and it is then that the vital role of the blood defenses comes into play.

Modes of Infection

It is the very minuteness of the disease-producing organisms that makes them so insidiously dangerous. Because of the large relative surface their smallness gives them, they are capable of astonishing reproductive and metabolic feats, so that they may produce many thousands of times their own mass in but a few hours. It has been estimated that one gram of *Streptococcus lactis*, one of the milk-souring germs, can hydrolyze up to 15,000 times its own weight in lactose in one hour. Obviously man reproduces at a snail's pace compared to this. And for him a proportional feat of metabolism would be to digest 1000 tons of food per hour!

Direct Contact. Bacteria can be conveyed from skin to skin, or they may adhere to objects or find refuge in the soil and from such sources reach the skin, or especially, breaks in the skin. Dust particles or droplets of moisture, such as those spread by coughing or sneezing, may convey millions of disease-producers through the air. These can evade the first-line skin defense by being transported directly to the delicate lung tissues or by settling on the relatively delicate mucous membranes of nose and throat. Water and food may carry bacteria into the digestive tract, where, if they pass the barrier of the acid stomach, they have easier access to the body tissues through the delicate intestinal villi. Finally, some organisms, among them the carriers of yellow fever and malaria, are transmitted by an intermediate host, such as the mosquito, thus evading all lines of defense and entering directly into the blood stream.

It is evident, considering the ubiquity of microorganisms, that the struggle of the body against disease is never-ending, and that without the chemical defenses of the tissues, the body liquids, and especially the common carrier, the blood, survival would be brief.

Attack and Immunity

It is a remarkable fact that certain microorganisms may kill a strong and robust man while an apparently inferior individual may

tolerate them with seeming impunity. Equally striking is the fact that epidemics of the same disease may vary in violence. Although the chemistry underlying these facts is incompletely understood, the biological principle of variation stands out clearly and is a major factor in the treatment of disease. It is also one of the reasons why problems of immunology are never finally solved. It has long been known that often the victim who has fought off a disease successfully has acquired a resistance or immunity against further attacks of the same disease. This fact, together with the observation that epidemics vary in virulence, sometimes has led to the practice of deliberately exposing persons to mild forms of smallpox in order to protect them against a possible deadlier outbreak in the future.

Antibodies

Protection of this nature is attributed to a variety of protective substances, or *antibodies*, carried by and perhaps in part produced in the blood. Bacteria cause most of their harm by producing potent toxins, which may destroy tissues locally or, carried throughout the body by the blood stream, may cause the most varied disturbances. The body is sometimes able to produce specific substances which render these toxins relatively harmless. Such antibodies are called *antitoxins*. The body is also able to produce substances inimical to the toxin-producing bacteria themselves, thus leading to their destruction and to the recovery of the host. Such antibodies are called *lysins*, *agglutinins*, and *opsonins*, depending on their action. Lysins, acting together with normal blood components, may cause foreign cells to swell and finally dissolve. Agglutinins cause the invaders to lose their motility and stick together. Opsonins are usually present in blood, but are formed in increased quantities during infection, and in some manner encourage the phagocytic action of leukocytes. The name *antigen* has been applied to the substances which stimulate the production of antibodies in an organism.

Since both the disease producer, or *pathogen*, and the host are living organisms — unless one

wishes to except the viruses — there is great variability of action and reaction on both sides. Since no two organisms are chemically identical, with the possible exception of identical twins, there is great variation in susceptibility between the representatives of different phyla, between classes and races, and even between individuals of the same species. By selection, this individual variation has resulted in a degree of racial immunity in human beings. Thus the white race is more resistant to tuberculosis than is the American Indian. Tuberculosis has been with the white race for centuries, selectively eliminating most of those chemically unable to cope with it, while the disease is relatively new for the Indians. The line of species immunity is usually more sharply drawn, as might be expected. Many pathogens afflicting human beings cannot live in the body fluids of other organisms, and vice versa. Thus poliomyelitis is never naturally transmitted to an animal, and canine distemper never attacks human beings.

Types of Immunity

Immunity may be innate or acquired, as we have seen. In either case, it is a result of the chemical composition of the body fluids. In innate immunity the organism is born with a chemical make-up inimical to a given type of pathogen. But even in acquired immunity, the genetic make-up must enable the organism to produce the necessary antibodies under the environmental stimulus of specific antigens. This latter situation has been exploited by medical science to help man in his struggle against disease. Utilizing the gradually learned fact that pathogens vary in virulence, man has learned to reduce the virulent effects of certain germs without materially reducing their antigenic action. Thus by injecting an individual with measured doses of certain toxins, with weakened bacterial cultures, with dead bacteria, or with combinations of these, the production of antibodies may be stimulated and the individual may become immune as he would by having the disease itself, but without exposing himself to the ravages of uncontrolled

bacterial multiplication in his body. Immunity thus attained is called *active immunity*, and differs in no way from that immunity acquired by actual previous exposure to the disease.

Another form of immunity is based upon knowledge of antibodies. Serum extracts from animals that have been immunized contain the antibodies which give them their immunity. Injections of such sera into another animal endow it with temporary immunity, but the immunity is *passive*, and in a relatively short time the antibodies are destroyed or excreted and the immunity is lost. Unlike what happens in the actively immune animal, the body tissues do not start to manufacture these antibodies. Thus the injection of antigens bestows no immunity immediately but stimulates the body into active production of antibodies, whereas the injection of antibodies bestows immediate immunity, but without active participation of the body, and hence without lasting effect.

Animals injected with increasingly large doses of toxins may be caused to produce great quantities of antitoxins for medical purposes, and their bodies may be repeatedly tapped as a rich source of antitoxin, without harm to the animal. Similarly, antibodies in the blood stream of an actively immunized expectant mother may be transmitted to the blood stream of the fetus, endowing it with passive immunity for a period lasting from several months to a year after birth. Thus immunity may be innate or acquired, active or passive, and it varies considerably from one biologic group to another. In whichever way it functions, it is our chief weapon against the multitudes of microorganisms that constantly beset us.

Progress in Immunology

The history of immunology reaches back to May 14, 1796, when an English country doctor, Edward Jenner, introduced the practice of vaccination. Country people had concluded from random observations that a cowpox infection, as contracted from infected cows by dairymen and milkmaids, bestowed immunity against smallpox. Jenner deliberately put this belief to the test by inoculating a boy with

cowpox and then, six weeks later, with smallpox. The boy proved to be immune, as did other individuals later so treated. The science of immunology thus made a beginning.

Although astute men had from time to time suspected that diseases were caused by microorganisms, for a long time it was generally assumed that these organisms arose spontaneously. Some men, like Lazaro Spallanzani in 1768, attempted to disprove this belief, but while Spallanzani showed conclusively that meat, heat-sealed in glass and boiled, did not decay, the question was not clearly settled until 1862. In that year Pasteur proved that boiled and sterilized broth could be preserved indefinitely even in contact with air and oxygen — that is, not sealed off, as in Spallanzani's experiment — if suspended dust particles were excluded. Pasteur placed broth in a tube with a S-shaped snout so that dust could not pass up the ascending arm. To prove that the broth was a suitable breeding medium, it was only necessary to tilt the flask so that a few drops ran to the low part of the snout and then back into the flask. The decay which followed showed that organisms picked up in the crook of the tube quickly multiplied and infected the rest of the broth. Experiments such as these led Pasteur to work on "diseases" of wine, and later, in 1865, on the pebrine disease of silkworms. These studies contributed vastly toward establishing the fact that many diseases are caused by living microorganisms.

Other workers, too, were doing their share, and it is perhaps to the Englishman Joseph Lister and to the German Robert Koch that we owe the final recognition of the living nature of pathogens. The use of chemical agents to destroy infectious organisms that had found their way into wounds, or still better, to prevent the entrance of microorganisms into surgical wounds, was tried and found effective. Antiseptic surgery (Gr. *anti* = against + *septikos* = produced by putrefaction) was soon followed by aseptic surgery (without sepsis) and made possible major surgery that previously would have meant almost certain death.

It was Koch who in 1876 obtained a pure culture of the anthrax bacillus, first discovered thirty years earlier. In 1882 he isolated the bacillus of tuberculosis. His methods of culturing bacteria laid the groundwork for the successful modern practices of immunology.

The discovery of the living nature of pathogens made it possible not only to destroy them but to discover specific agents that would destroy them within the body of the host without seriously damaging him. Advances in the search for "magic bullets" have recently been spectacular. The search was begun early in this century by the German bacteriologist Paul Ehrlich, who in 1910 discovered the famous 606 or salvarsan, an arsenical compound found highly effective in the treatment of syphilis. No such specific chemicals ever found have been ideal, but the control of many diseases previously incurable or stubborn has now become possible. Since 1935, when the effectiveness of sulfanilamide in checking streptococcus was discovered, several thousand new sulfa compounds have been derived, many proving to be highly effective specifics. The most effective to date are the now widely known and praised sulfanilamide, sulfapyridine, sulfathiazol, sulfadiazine, and sulfaguanidine. Specific germ killers produced by certain molds, such as penicillin and streptomycin, have proved invaluable in combating certain infections. But in the midst of these successes, peculiar variations in the effects of these drugs on both parasites and host remind us that bacteria may mutate too, and so may acquire resistance to the drug. Moreover, a specific drug may prove highly effective in controlling a certain type of infection in one patient, while it may prove disastrous when applied to another.

Bacteriophage

In 1917, the Frenchman d'Herelle bestowed the name *bacteriophage* on what he believed to be an ultramicroscopic living organism capable of destroying certain specific bacteria. Similar phenomena had previously been observed by others as early as 1896, when Hawkins found that the waters of the Jumna River of India

were self-purifying. That there are substances capable of destroying bacteria has been amply verified, as has been the fact that they are autocatalytic, if not autotrophic. Traces of bacteriophage placed in a suitable bacterial culture destroy it and even clear the cloudy bacterial suspension. Minute traces from such a cleared suspension are again capable of "infecting" a large quantity of the same sort of bacteria, and so on, indefinitely. The phage appears to be a virus. Most authorities now incline to the belief that the bacteriophage is autocatalytic, causing bacteria to decompose in such a manner as to liberate additional quantities of itself.

The Struggle Against Disease

The struggle against invasion by destructive microorganisms is keen and constant. Survival amid hosts of pathogenic parasites is possible only because of a relay of defenses evolved over the ages by selective adaptation to similarly adaptive pathogens. The defenses of the human body are multiple and varied. Mechanical defenses such as the skin, hair, and beating cilia ward off or remove many bacterial organisms. Fatty skin secretions, tears, and acid stomach secretions are inimical to the growth and survival of many bacteria, as is increased body temperature, or fever, by which the body frequently fights infection. The last and main line of defense is the blood, with its many forms of antibodies, and possibly bacteriophage, working in conjunction with the vital defenses of the phagocytic leukocytes. These represent the heritage by which man survives.

THE RESPIRATORY SYSTEM

The lungs of mammals, and of man, are among the most efficient found in the vertebrates. The windpipe or *trachea* forks into two *bronchi*, which in turn branch to produce vast numbers of smaller tubes or *bronchioles*, each terminating in an elongated sac, made up of small spherical bubbles called *alveoli*. These are the real units of respiration, and in man they number about 700 million. Each alveolus, 10 μ in diameter, consists of simple plate-like epithelial cells, which are also the walls of the

capillary network. Blood flows from the pulmonary artery into these capillaries, which then reunite to form the pulmonary veins leading back to the heart.

The average person breathes in about 12,000 liters of air per day, or the amount contained in a room measuring 40 feet square and 8 feet high. Since a single breath of air may contain from a million particles of dust in country air to as many as 50 billion particles in city air, the dust, transformed into mud in the lungs, would soon fill them solidly were it not for cleansing and filtering devices. A screen of hair in the nostrils guards against inhalation of coarse particles, while the mucous membrane of the trachea is covered with millions of beating cilia which propel dust particles upward into the throat, whence they are expelled. Very dusty work, however, brings in more dust than the system can expel. Workers in siliceous quarries may accumulate dangerous quantities of invisible silica particles and contract the deadly and incurable inflammation of the lungs called silicosis, which usually ends in pulmonary tuberculosis.

Mechanism and Control of Breathing

As in all mammals, man "draws" air into his lungs by lowering his diaphragm or by raising his ribs, thus inflating the alveoli. Although these respiratory movements, unlike those of the heart, are under voluntary control, there is also extensive provision for automatic control, essential during sleep. The coordinator is the respiratory center of the medulla oblongata. As the carbon dioxide in the blood rises, motor impulses from the medulla stimulate the muscles of inspiration and we inhale. These movements stimulate nerve endings in the lung, initiating impulses which inhibit the action of the medulla, relaxing the inspiratory muscles. Exhalation follows. This cycle accounts for the rhythmic and automatic breathing characteristic of deep sleep.

The Chemistry of Respiration

Since the flow is always from the greater to the lesser concentration of the diffusing mole-

cule, oxygen passes from the air in the alveoli into the capillaries around them, and carbon dioxide from these into the air. The red blood cells contain a high concentration of hemoglobin, which enormously increases the oxygen capacity of the blood. Arterial blood carries up to 20 volumes per cent of oxygen, of which only 0.3 per cent is in solution. This amount normally remains quite constant, but the amount carried as *oxyhemoglobin*, that is in combination with hemoglobin, fluctuates between 12 per cent in venous blood to the 20 per cent maximum in arterial blood. The carbon dioxide content of the blood varies between 50 to 56 volumes per cent, part in solution and part in chemical combination as bicarbonate of sodium or potassium.

Chemically combined oxygen is of little use to the tissues, but a precise mechanism frees it as needed, while it is quickly removed from solution in the lungs to make way for further absorption. This chemical mechanism is closely associated with the absorption and release of carbon dioxide (Fig. 467). The hemoglobin combines with oxygen when in the presence of an abundance of oxygen, and releases it when in contact with tissues or fluid low in oxygen. The CO_2 is carried principally in the plasma, but to some extent in the red cells, in the form of bicarbonate (K or Na), and the equilibrium between carbonic acid and bicarbonate in the blood plasma, so important in the acid-base balance of the body, shifts toward the former in the lungs (so releasing CO_2) and toward the latter in the systemic capillaries where CO_2 is entering the blood. In other words, an excess of carbonic acid, produced by entrance of CO_2 into the blood, leads to a shift toward bicarbonate; whereas an excess of bicarbonate, produced by the loss of CO_2 from the blood in the lungs, leads to a shift toward carbonic acid and the loss of more CO_2 .

This chemical device is not foolproof. Carbon monoxide, of auto exhaust notoriety, combines 210 times as readily with hemoglobin as does oxygen. Even small traces of CO absorbed by the blood destroy its capacity to carry oxygen. Nevertheless, both physiologi-

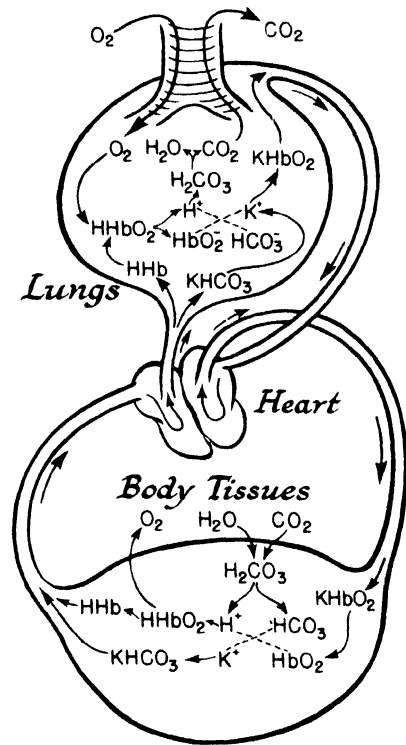


Fig. 467. The chemistry of respiration.

cally and chemically, the respiratory system surprisingly well meets the exacting and variable demands of the organism under widely differing environmental conditions.

THE EXCRETORY SYSTEM

Although the human kidney is no larger than a fist, its interior is a maze of approximately one million globular filters and about 20 to 30 miles of tubules. Each unit or nephron (Fig. 468) consists of a globular Malpighian body and a greatly convoluted uriniferous tubule. The entire cortex or outer layer of the kidney consists of perhaps a million of these capsules, while the medulla or inner region is a mass of collecting tubules leading into a common funnel-like cavity which tapers quickly to form the ureter.

How the Kidney Functions

Blood enters the kidney through the renal artery, carrying its usual freight of dissolved

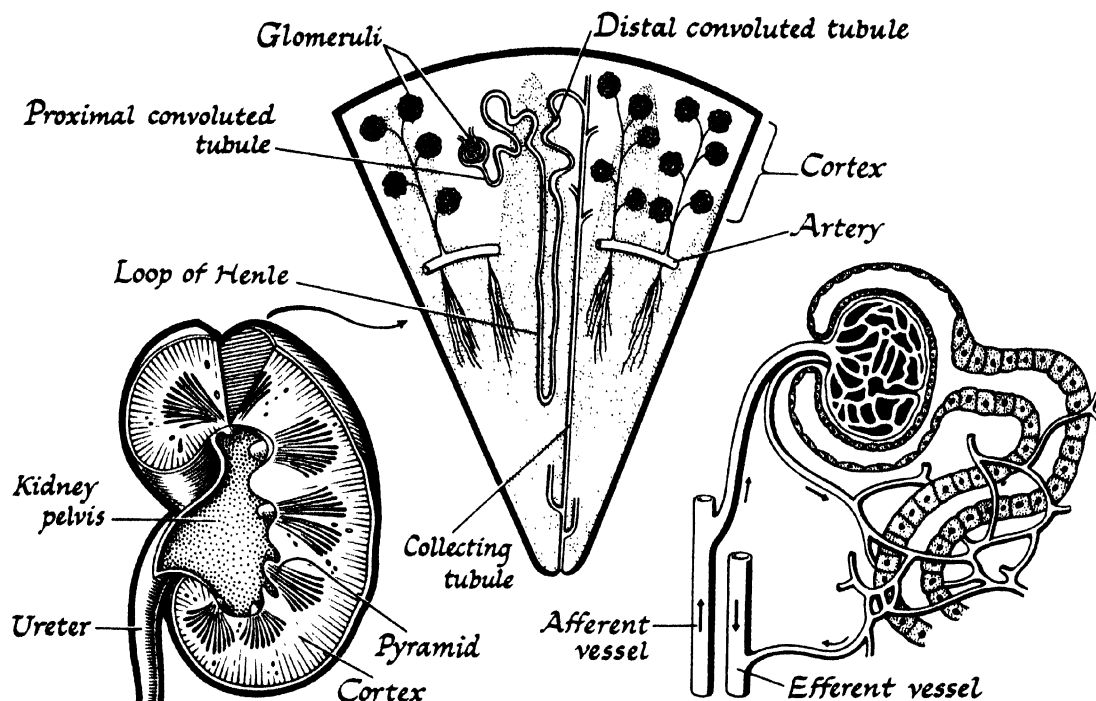


Fig. 468. Diagram of kidney and nephron. The whole kidney is shown at the left. The central figure shows an enlarged view of a wedge cut out of the kidney. At the right is a diagrammatic presentation of a single glomerulus within its Bowman's capsule, the nephric tubule, and the surrounding blood vessels.

and chemically bonded bases, its nutrient molecules, wastes, blood proteins, hormones, and enzymes. The kidney sorts the "good" from the "bad" by a combination of general filtration through the glomerulus and Bowman's capsule, followed by selective reabsorption and further secretion, as yet incompletely understood, in the uriniferous tubule. Blood pressure forces a portion of the blood plasma, with all its soluble freight save some blood proteins, into the nephric tubule. Forming the walls of each tubule are many thousands of cells, which pick up 59 parts out of every 60 filtered into the tubule, and secrete them back into the surrounding capillaries. These capillaries receive their blood supply from a small vessel that emerges from the glomerulus of the same nephron. Thus a molecule of water filtered out of the blood in the glomerulus, may, a few seconds later, find itself back in the same blood stream again.

Since the absorption and secretion in the cells of the tubule is selective, the fluid has changed drastically by the time it leaves, and

the kidney of the healthy body has removed from it much of the water, all the nutrient molecules, and even some of the wastes that might better have been left in it. Nevertheless the fluid, now called urine, contains a large percentage of undesirable wastes, which are ultimately excreted.

The rate of filtration and secretion in the kidney is partly a function of blood pressure and partly under the control of hormones. But the kidney may also influence blood pressure. Reduced kidney action due to lowered circulation causes it to release *renin*, which increases arterial pressure. Other hormones, among them products of the posterior pituitary lobe and the adrenal cortex, play a role in controlling the functioning of the kidney.

Abnormal metabolism or malfunctioning of the kidney can be determined by making a chemical analysis of the urine. Excessive quantities of sugar in the blood, due, for example, to incomplete sugar metabolism owing to lack of insulin in diabetes, causes excretion of sugar. Evidently the tubule cells are incapable of re-

absorbing the excess glucose. Infections may damage the linings of the uriniferous tubules and produce similar results. Proteins in the urine may indicate increased permeability of the blood vessels of the glomerulus as a result of inflammatory changes. Other defects of metabolism or kidney action may be similarly diagnosed. The kidneys have a considerable safety factor and can bear so much more than their normal load that a man can live with but one kidney. But the loss of both results in swift death.

BRAIN AND NERVOUS SYSTEM

Essentially, the human nervous system is much like that of other higher vertebrates, and consists of brain, spinal cord, autonomic system, sensory and motor nerves, and ganglia. Because of this similarity, it will not be necessary to discuss all parts of this system here, since their general aspects were taken up in Chapter 18. But the crowning evolutionary achievement which has given man his preeminence is his brain. While all mammals have large brains, man stands as far above the average of this group as the mammal does above the average invertebrate. The human brain differs from that of higher vertebrates only in size and complexity, but these differences are of prime importance.¹

Lower Brain Centers

Like that of all mammals, the brain of man is divided into three main parts, the two lowest

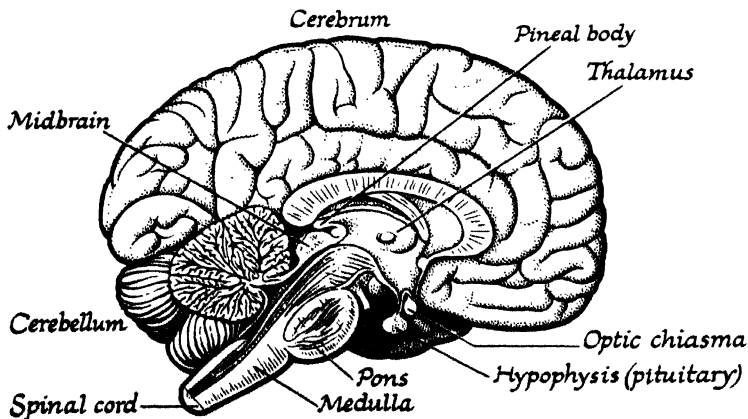
¹ For a discussion of the general plan and the divisions of the mammalian brain, see pages 403-407.

of which are the *medulla oblongata* and the *cerebellum* (Fig. 469). The former of these is an enlarged continuation of the spinal cord but with special functions. In addition to serving as a pathway for nerve fibers on their way to and from the higher brain centers, it performs certain very important automatic functions. Thus it includes the cardiac inhibitory center, the respiratory center, and the center responsible for the constriction of the blood vessels. Many other reflexes, such as coughing, sneezing, vomiting, and the movements of the digestive organs are under the control of the medulla. Lowest of the three main portions of the brain on the evolutionary tree, and not a seat of consciousness, it is essential in keeping the machinery of the body going.

The second largest part of the brain in man is the cerebellum, chiefly a reflex center unconsciously helping to coordinate complex muscular movements, especially in maintaining equilibrium. The cerebellum is a kind of relay station and mixer combined. Here sensory impulses from the semicircular canals of the inner ear, the organs of balance, and others from the muscles and tendons, are combined with regulating impulses from the higher parts of the brain and translated into motor impulses which go to all the motor centers of the body.

Several other parts of the brain may be mentioned briefly. Directly beneath each half of the cerebrum, the most highly developed portion of the brain in man, is a stalked *olfactory lobe*, of great importance in mammals with a keen sense of smell, such as the dog or the deer,

Fig. 469. Median aspect of halved human brain. Only a few of the essential features are named.



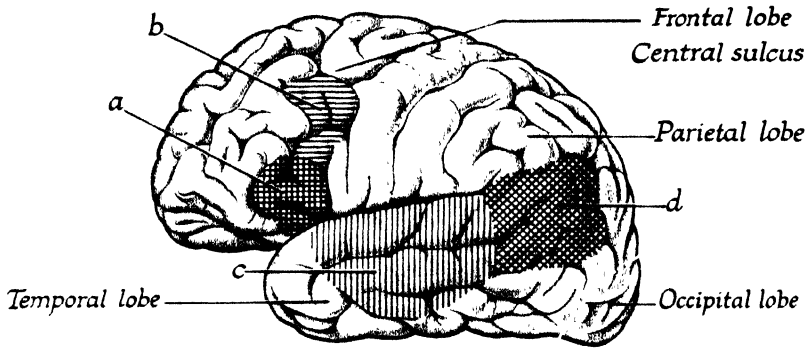


Fig. 470. The human brain. The cerebrum has covered all the rest. Important regions and areas are marked. Areas marked *a*, *b*, *c*, and *d*, are speech centers.

but quite simple in man. At the base of the cerebrum is a large egg-shaped mass, the *thalamus* (Fig. 469), which serves as an important relay station between cord, brain-stem, and cerebral cortex. Clusters of synapses called *nuclei* are important in regulating unconscious functions such as coordinating muscular activities, conducting uncritical pain sensations, and regulating body temperature. A lower portion of this, the *hypothalamus*, is said to function in regulating simple emotional states, such as fear and anger, and in controlling sleep. Just behind the thalamus lies a short portion of the brain-stem, the *midbrain*, which is mainly a relay for visual and auditory reflexes. Finally, a mass of fibers connecting the halves of the cerebellum and joining the midbrain and the medulla is known as the *pons* ("bridge"). But none of these is the seat of consciousness, any more than the medulla is.

The Cerebrum

This precious faculty resides in the *cerebrum*, the seat of higher coordination, perception, and cognition. Indeed, the human brain is mainly remarkable for the enormous bulk of its cerebral tissue. Divided into two so-called *hemispheres*, the cerebrum has overgrown most of the other brain regions and fills most of the enlarged brain case (Fig. 470). The human cerebrum is in two distinct layers, the outer cerebral cortex, only two millimeters thick, which with its maze of synapses represents the heart of the thinking mechanism, and the massive

inner white matter, consisting of interlaced and crisscrossed bundles of nerve processes, connecting parts of the brain with each other and with nerves leading to all parts of the body.

To make room for the increasing mass of cerebral neurons without an undue increase in skull size, the cerebral cortex of higher mammals, and especially of man, is thrown into many folds and wrinkles dividing the cortex into four clearly recognizable lobes which correspond to the bones of the skull. These are the *frontal*, the *parietal*, the *temporal*, and the *occipital* lobes, each with particular regions known by various experiments to serve specific functions. There are, however, large areas whose specific function is not known, but which are believed to serve as mediators between other areas.

The *frontal lobe* of the brain is divided from the parietal lobe directly behind it by a deep fissure, the *central sulcus*. The precentral area immediately in front of this fissure controls the conscious movement of various parts of the body. Electrical stimulation of certain parts of this area causes such phenomena as bending the arm or wiggling the toes. The frontal lobe is also the site of two of the four speech centers (*a* in Fig. 470). Injury to the frontal motor speech area causes loss of the power to speak. Injury to the sensory area (*b*) destroys the ability to form the letters of a written word.

The foremost area of the frontal lobe is the *prefrontal*, often called the "primary association area." It appears to be concerned with the complex function of memory and with concepts

of the future, and somehow with conscience and the sense of duty and moral obligation. Two American brain surgeons, Freeman and Watts, have helped cases of extreme psychopathic anxiety by an operation known as prefrontal lobotomy, in which the fibers projecting to the frontal areas from the lower brain centers are severed. The operation also impairs the ability to project into the future, and to feel duty and obligation, the main causes of anxiety. Directly behind the central sulcus, in the parietal area, is the *primary sensory area*. Here electrical stimulation causes sensations of tickling in specific regions of the body, as in the hand or foot.

The *temporal lobe* contains the cerebral *hearing* centers and the *auditory speech* center (c in Fig. 470). Injury to the latter area results in inability to recognize spoken words, although it does not impair hearing or the ability to read and write words.

The *occipital lobe* is the projection area for vision. Electrical stimulation of the area produces sensations of bright flashes of light or even definite visual sensations, according to the reports of patients undergoing brain operations with only local anesthesia. Destruction of the occipital cortex results in total blindness in man. But partial destruction of certain areas of it may leave vision itself unimpaired yet completely obliterate all memory connected with the objects seen. Thus a patient may be able to see a chair, a typewriter, or even a close friend, but not be able to identify what he has seen until he has established more than visual contact.

How the brain works is at best but partially understood, and it may well be that we shall never chart all its complexities. While it is possible to find out by experiment the functions of many parts of it, this is far from the whole story. We must remember that the brain is a highly coordinated unit, and that the centers which we know a little about, especially those in the cerebrum, are merely focal points of activity, quite powerless to do their work without the cooperation of many other parts of the brain. Nor should any one function

be thought of as tracing back solely to one of these focal points. Nevertheless, the present knowledge of focal control centers is of great value in the diagnosis and treatment of brain diseases and injuries, and it is certainly a long step toward further knowledge.

PATTERNS OF BEHAVIOR

Learning and Retention

Very little is known about the functioning of the brain in learning and retention, though it seems clear that some sort of permanent or semi-permanent change in the electrochemical structure of the brain must occur when we learn. However, a characteristic of the brain has recently been discovered which may play a vital role in such changes. This is the existence of so-called *brain waves*. Electrodes placed upon the head pick up rhythmic impulses, which can be amplified like radio waves and reproduced either as a sound or as a visible pattern. These show that the brain is ceaselessly active, even in sleep. The pattern of the waves changes with varying emotional states, during sleep, or during mental activity. The pattern is also distinctive in certain diseases, such as epilepsy. Finally, and perhaps most surprising of all, the brain waves of any individual are as distinctively his as are his fingerprints. The brain is the governing center not only of our various animal activities, but also and especially of those essentially human qualities such as cognizance and reasoning. Moreover, the fundamental brain structure and its consequent mode of action both appear to be as much personal characteristics as any other physical feature.

REFLEXES AND INSTINCTS

Reflexes, which appear to govern the lives and behavior of many invertebrates, play a relatively minor role in the major actions of man, as of other mammals, but even here many minor yet collectively important reactions are so controlled. Reflexes are automatic and relatively unmodifiable responses which in man

have been largely sublimated by adaptive responses. A reflex is a short circuit of neural impulses, in mammals usually involving at least *three* neurons at the level of the spinal cord or the lower brain centers. Those involving lower brain centers include more neurons than those of the spinal cord and result in more complex behavior patterns.

Of the many reflexes displayed by man, only a few need be cited as examples: the eye blinks at the approach of an object; reflexes jerk finger, hand, or foot away from hot or sharp objects; the lens of the eye accommodates by a reflex so as to focus a sharp image on the retina; the pupillary reflex adjusts the opening of the iris to the amount of light prevailing. The usefulness and selective value of these reflexes is evident. Apparently less useful are such reactions as the knee jerk reflex.

Instincts

The term *instinct* has long been employed to designate unlearned forms of behavior that simulate intelligent action. Many so-called instinctive acts have been analyzed as sequences of simpler reflexes, so that we have come closer to understanding them. The acts remain automatic and unlearned, but not much more mysterious than a pupillary reflex or a knee jerk. For this reason, the term instinct has fallen into disfavor in many quarters, and is said to be no longer necessary since we now know the nature of the activating stimuli. But used in reference to a complex chain of *interrelated reflexes*, it is still useful.

In lower animals, instincts are often of prime importance to complex behavior patterns. We have already described the bathing and feeding instincts shown by a group of fledgling jackdaws which had no opportunity to learn the behavior they displayed (pages 156–157). Most birds automatically sing the songs characteristic of their species without benefit of tutor. Many birds build their nests as their parents did even though raised in captivity where they never saw a nest. Likewise, a female rat, during the period of estrus (heat), shows greatly increased activity and may cover many miles in a day.

As a result, her chances of meeting a mate are improved. And when she does, she performs certain series of unlearned reflex actions which may result in copulation.

The instinctive mechanism is effective under limited and normal environments. But altered conditions may quite misguide the reaction pattern. A wild fox instinctively carries her young out of her den if she feels herself “discovered,” and transfers them to a new and secret place. In captivity she may also carry her young out of her box if she is disturbed, but if no new “den” is provided for her to hide them in, she scatters them about the enclosure and leaves them to die. She may even become so agitated and confused that she devours them. In man, however, chains of reflexes have been increasingly overlaid and obscured by learned and intelligent behavior, though reflexes, simple and complex, are important in subordinate mechanisms.

Conditioned Reflexes

An example of a simple reflex is salivation in response to food placed in the mouth. This is an inborn reaction. But it does not take long for a child to associate the smell of food with the feel of food in the mouth, so that the mere smell of familiar foods suffices to cause salivation. This is called a *conditioned reflex*, for a new stimulus has been substituted for the original one. It is even more striking when a rather unnatural stimulus, such as the sound of a bell, is substituted.

In man a surprising number of reflexes have become conditioned, and such responses, in contrast with the innate reflex or instinctive behavior of most lower organisms, largely govern our lives. Unaccountable likes and dislikes, unreasoning prejudices and inclinations have their roots in such early conditionings. Thus a child can be given an unreasoning and ingrained fear of a rabbit, or any other animal, if subjected to frightening noises each time a rabbit is presented — and the noises need by no means appear to come from the rabbit. In due time, sight of the rabbit alone elicits a fear

response. The unreasoning fear can be overcome again by associating the rabbit with a pleasant experience, such as eating. Again, in due time, and quite as unreasonably, the rabbit will be welcome.

Such responses are by no means limited to children. "Reasoning" adults will respond in precisely the same manner, and frequently do, as instanced by the prevalence of many kinds of habits and prejudices.

Habits

Growing out of conditioned reflexes are certain tendencies to behave or respond in certain ways, and these tendencies are generally called habits. In man, these habitual responses become of immense and pervasive importance. He becomes accustomed to eat, sleep, dress, and go forth at accustomed hours. He picks at random from a shelf of books a novel or a treatise on oriental art because he is predisposed by a series of habituations to an interest in one rather than the other. He is a Democrat or a Republican, a liberal or a conservative, a scholar or a man of affairs partly because he is inclined by a complex of tendencies, habits, and prejudices in one direction, not another. The basis of habit is the conditioned response.

It is widely held that learning consists largely of acquiring conditioned responses. It is impossible to say how true this is, but certainly the theory throws light on the nature of speech. Since speech, as a system of communication, makes possible the exchange and transfer of individual experience, it is the prime agent which, for good or bad, has made possible the

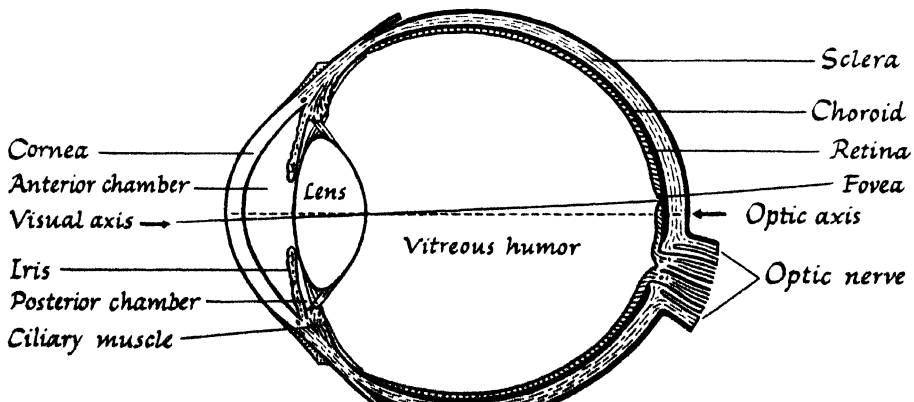
welding of human individuals into the organized units upon which civilization rests. Words, which constitute speech, are sometimes substitute stimuli for original objects or events. Thus even a word may eventually elicit a conditioned response. The word "food" may initiate a salivary reflex after suitable conditioning — and quite possibly is doing so at this moment with the reader of this book. A fuller understanding of such relationships may have a profound influence on the further evolution of man.

ORGANS OF SPECIAL SENSE

The Eye

Of all animals, only birds and cephalopods can match the mammals in vision, and the human eye ranks among the best. Dogs are colorblind, and many animals are unable to discriminate between many colors which the normal human being can distinguish. The same degree of excellence applies to acuity of vision in man though some birds and mammals exceed even man in keenness of sight. A delicate and relatively fragile organ, it is well protected by a bony socket, eyebrows, eyelids, eyelashes, and tear glands. Reflex closure of the eyelids shortens the reaction time in emergencies, and automatic winking maintains the necessary moisture, furnished by the tear glands above the eye. In the inner corner of the eye is the rudiment of the third eyelid found in lower vertebrates. The spheroid eyeball moves freely within its lubricated and fat-cushioned orbit, governed by three pairs of antagonistic muscles.

Fig. 471. Horizontal section through the axis of the human eye.



Structure. The wall of the eyeball consists of three distinctive layers, the outer horny *sclera*, the pigmented and vascular *choroid*, and the inner light-sensitive *retina* (Fig. 471). The white, tough sclera changes in character toward the front of the eye to form the more vulnerable but clear and transparent *cornea*.

The pigmented choroid coat is an optical insulator which keeps out stray light, and its blood vessels supply the other layers. At the front of the eye, this layer is modified to form the *iris*, a diaphragm with a constricting central opening, the pupil, which by reflex (see pages 529-530) regulates the amount of light entering the eye. Behind the iris is the lens, suspended by ligaments anchored to the inner margin of the choroid coat. The chamber between lens and cornea is filled with the watery aqueous humor, and a larger cavity behind the lens is filled with the thick jelly-like vitreous humor. The entire back cavity is lined by the retina.

Accommodation. In mammals, accommodation for vision at different distances is achieved by changes in the thickness in the lens,¹ which is elastic, and under the control of small attached muscles becomes thicker for close vision and is stretched thinner for distant vision. Unfortunately, several things can go wrong with this delicate mechanism. With advancing age, tissues tend to lose their elasticity and plasticity and the lens may become unable to become round enough for close accommodation, so that the individual becomes farsighted. Some people, born with a barrel-shaped lens which projects a point as a line, are said to be *astigmatic* (Gr. *a* = against, or not + *stigma* = point). (But most astigmatism is due to unequal curvatures of the cornea.) Again, the eyeball may be too long or too short, causing nearsightedness or farsightedness. All these defects can be corrected by properly fitted glasses.

The Retina. The *retina* is an outgrowth of the brain and consequently is nervous in structure (Fig. 472). It is composed of three main layers. The inner one, next to the center of

the eyeball, consists of conducting neurons or ganglion cells, the second consists of bipolar cells, and the third or outer layer of the actual light-receptor cells, the *rods* and the *cones*. Near the visual axis lies a slight pit or depression where vision is most acute, the *fovea centralis*. Toward the nose from this lies a blind spot where the nerve fibers from the entire retina converge to form the optic nerve. In normal vision each eye is automatically trained on an object so that the image falls upon the fovea, for only here is vision sharp and full. The outer edges of the retina produce only a fuzzy image, poor in detail and color. Normally this escapes notice, since one's imagination fills in the missing details and the eye moves constantly from point to point so that each can be analyzed by the fovea.

The *rods* and *cones*, the actual light receptors, supplement each other. The peripheral retina consists largely of rods, the intermediate zone has both rods and cones, whereas the fovea is equipped mainly with cones. These, though less sensitive to light, have acute vision and color discrimination. The rods are highly sensitive to faint light stimuli but are color blind. Thus a faint star caught out of the corner of the eye becomes quite invisible when we look straight at it. Some nocturnal animals, such as bats and possibly mice and rats, are equipped with rods only.

The nervous connections of these two types of visual cells partly explain their difference in function. It is claimed that there are two types of bipolar cells, the *diffuse* and the *midget*. The former collect impulses from more than one primary neuron (rod or cone) and may serve as many as two hundred rods in the periphery, so that light falling on all two hundred produces but a single nerve impulse. The midget bipolar cells, on the other hand, synapse one-to-one with rods or cones, chiefly the latter. This one-to-one ratio also holds for the cells of the middle and ganglionic layers, for each midget polar neuron makes a synaptic connection with a monosynaptic ganglion cell. Such an arrangement produces more acute vision, but has less sensitivity. This arrangement is

¹ See also pages 331-332.

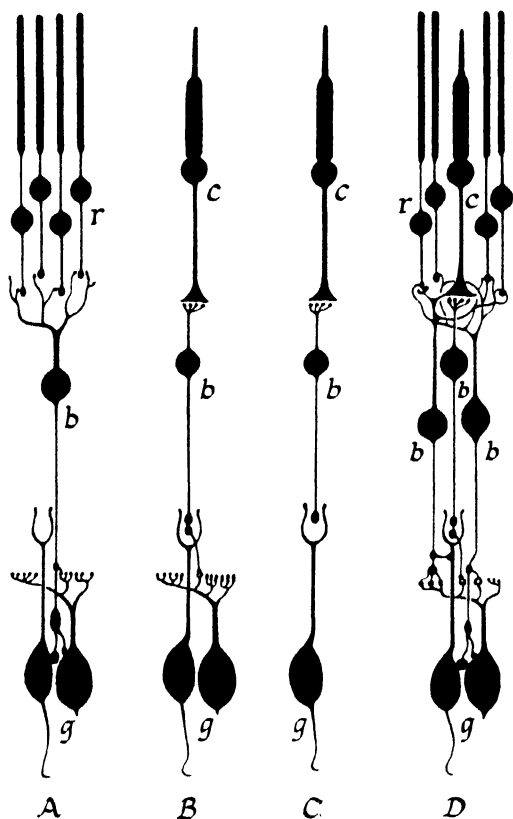


Fig. 472. Retinal cells, showing several types of connections. *A.* Four rods connected with a diffuse bipolar cell leading to several ganglion cells. *B.* Single cone connected with midget bipolar cell leading to two ganglion cells. *C.* Single cone connected with midget bipolar cell leading to single ganglion cell. *D.* Mixed relationships of rods and cones. *r*, rods; *c*, cones; *b*, bipolar cells; *g*, ganglion cells.

especially characteristic of the central region of the fovea, where the cones are extremely slender and closely packed and there are no rods, blood vessels, nerve fibers, or other retinal layers. Here also the cones are very close to the surface upon which the image is projected.

Theories of Vision. It is not known just how the eye sees, and while various theories have been suggested, they do not account for all the observed facts. One of the most favored theories is the *photochemical theory* of Hecht, which applies primarily to rod vision. According to this hypothesis, a chemical substance, the so-called "visual purple," breaks down

under the action of light and is rebuilt in the dark. Hecht has postulated that the amount of this substance broken down determines the strength of the nerve impulse and consequently the intensity of a perception. Recently Crozier has proposed a supplement to this theory, which accords with the classical all-or-none law of muscle and nerve responses to the effect that a cell responds fully or not at all, so that in vision the intensity of perception depends upon the number of receptor cells involved.

Theories of color vision are less well validated. That of von Helmholtz, in part a revision of earlier hypotheses, still appears basically sound. This theory postulates only three kinds of color receptors, red, green, and blue, perception of all other colors resulting from various combinations of these. The theory is supported by recent experiments made by the American physiologist Granit on *Limulus* and certain mammals. It is not known what electrochemical mechanism may be responsible for color discrimination.

Likewise, much is still to be learned about after-images and color blindness. After-images are visual perceptions which continue for a short time after the eyes are closed or an object is no longer in view. They are common after looking at a bright object like the naked filament of an incandescent light, though such violent stimulation is not necessary. Staring at an object, then closing the eyes, will produce the effect. If the object is colored, the after-image will appear in the complementary color; a red object will produce a blue-green after-image. It may be that the three types of receptors send a constant series of impulses to the brain even when *not* stimulated by light, and stimulation of one type by a specific color increases the tempo of its activity, perhaps increasing the frequency of impulses. Cessation of the stimulus may then cause consequent subnormal activity of the recently overactive receptor, leaving the complementary color to dominate.

Eye Coordination and Perspective Vision. Through the brain which they serve, the two

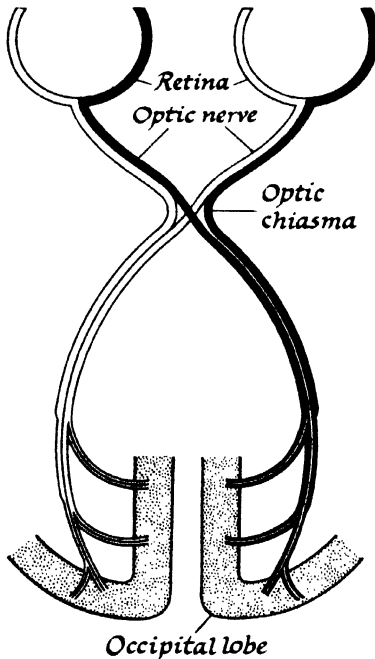


Fig. 473. Optic pathways, showing the chiasma, the crossing of the optic nerves. Note that a portion of the retina of each eye is connected with each occipital lobe of the brain.

eyes are intimately linked, so that they move and respond in unison (Fig. 473). Because of the incomplete crossing of the optic fibers at the juncture of the optic nerves, the fibers from the left half of each eye lead to the left occipital lobe, and those from the right half lead to the right occipital lobe. Upon this anatomical basis perspective vision rests. Since each eye automatically converges on the point of scrutiny, each retina becomes so oriented that the image of that point falls upon an exactly corresponding spot in each retina. The point, although received as two images in two eyes, is perceived as one, presumably because both groups of impulses lead to the same side of the occipital lobe of the brain. If the point images fall upon non-corresponding regions of the two retinas, two spots are "seen," as can be demonstrated by looking at the point "cross-eyed." The images of a three-dimensional object produced in the two eyes cannot be identical, since they are dif-

ferent views of the object, seen from different angles. Superimposed on the occipital lobe, the differences are translated by the brain to produce the effect of depth, thus producing three-dimensional or perspective vision.

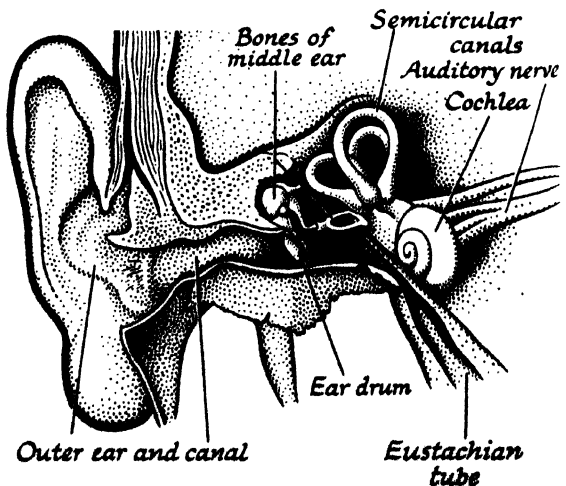
The Ear

Man's range of hearing is more limited than that of certain other animals. Bats, mice, and many birds can perceive sounds to which the human ear is deaf — and a type of dog whistle makes a sound which human beings cannot hear. But within his range, man is probably capable of greater discrimination of sounds than most other creatures. How much of this ability is acquired and how much inherited is still a moot question.

The complex hearing mechanism in man consists of three parts (Fig. 474), the outer, visible ear and the auditory canal leading to the eardrum; the middle ear, containing three minute bones, the hammer (*malleus*), the anvil (*incus*), and the stirrup (*stapes*), which serve as relays and modulators of sound vibrations; and the inner ear, containing the *cochlea*, the fluid-filled coiled set of tubes within the bony skull. A slender duct, the *eustachian tube*, leads from the chamber of the middle ear to the pharynx, and permits equalization of air pressure on both sides of the eardrum.

The Inner Ear. By far the most intricate part of the ear is the inner ear, which consists

Fig. 474. The ear, showing outer, middle, and inner portions in cross-section.



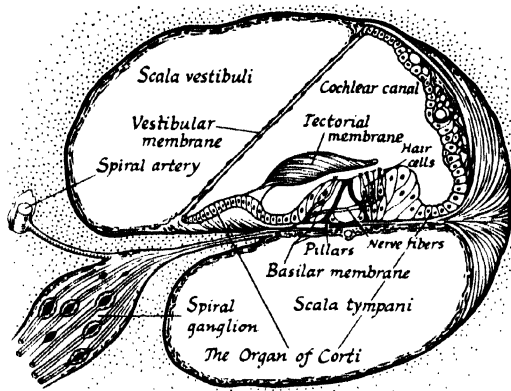


Fig. 475. The cochlea, showing principal structures.

of a group of bony tubes with a membranous lining, several of which, including the *semi-circular canals*, are primary organs for sensing balance, while others, coiled like a snail-shell, form the ultimate organ of hearing. Within the central pillar of this spiral lies the *spiral ganglion*, the focus of the auditory neurons running into it from the chamber of the cochlea (Figs. 475, 476). The cochlea consists of three canals or sections, one above the other. The central *cochlear* or *canal* is a blind tube, slightly wider toward the apex of the cochlea than at its base. The upper and lower canals communicate with each other at the apex and are filled with a lymph-like fluid. The central canal differs from these fundamentally, for it is an outgrowth of the brain itself, like the linings of the semi-circular canals. Together with the cochlear canal they are referred to as the *membranous labyrinth*. They are also filled with fluid.

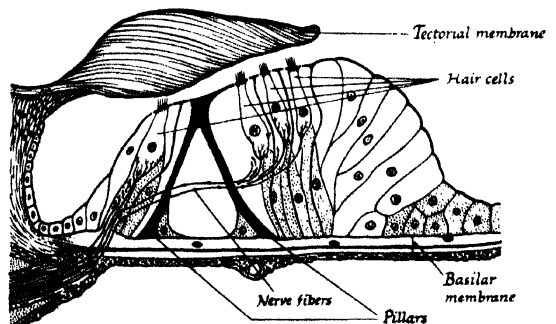
The cochlear canal rests upon a spiral shelf of bone. Its roof is a delicate membrane and its floor a fibrous one. Upon the latter, or *basilar membrane*, rests the complex sound-receiving and -analyzing membrane, the organ of Corti.

The Organ of Corti. Running the length of the cochlear canal, and resting upon the basilar membrane, there is a continuous series of extremely delicate hair-cells making up the organ of Corti. These rows of cells bear short hairs, the upper ends of which appear to touch or be embedded in the almost structureless *tectorial membrane* which arches over them like a roof.

Prevailing Theory of Hearing. Toward the apex of the cochlea, the basilar membrane is broader and thinner, and the organ of Corti more massive. It has been established that sounds of different frequency cause maximal vibration of this membrane at different points along its length. Thus high notes chiefly affect the lower and narrower end of the basilar membrane, where it probably has a higher natural period of vibration, and low notes the upper and wider end, where the period would be lower. So, as the pitch of a note rises, the vibration center on the basilar membrane shifts from the apex toward the base. Increased intensity produces a greater spread of excitement over the basilar membrane, thus involving a greater number of receptors in a given region, but the peak of vibration remains approximately in the same region, whether the tone is soft or loud. This again may be an expression of the all-or-none law.

As the basilar membrane vibrates, the hair cells upon it vibrate and their hairs move against or are damped by the tectorial membrane, stimulating the hair cells and, in turn, the surrounding network of auditory nerve endings. In this manner groups of nerve impulses arise, with peaks at different regions of the cochlea for different sound frequencies, and covering zones of various widths on either side of the peaks, accounting for the ability to distinguish between tones of different pitch and intensity, respectively. At best, modern theories of hearing are incomplete, a fact not surprising when we consider that the cochlea, though smaller than a pea, can respond to a frequency range from 16 up to 20,000 vibrations per second.

Fig. 476. Portion of cochlea, showing basilar membrane, organ of Corti and tectorial membrane.



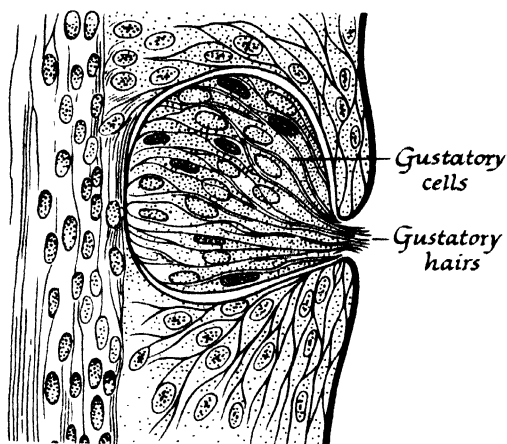


Fig. 477. Vertical section of a taste bud.

Deafness, partial or complete, may result from failure of any part of the hearing mechanism. A ruptured eardrum will lower sensitivity. Calcification or disintegration of the small bones of the middle ear may hinder the transmission of sound. Such forms of partial deafness are amenable to hearing aids, since sound vibrations led through the ear to the auditory canal may be amplified or sound may be transmitted directly to the temporal bone and through it to the cochlea. Infection of the cochlea may cause destruction of the organ of Corti, producing permanent deafness, either total or localized in pitch. Prolonged exposure to intense sound of a given pitch has been shown to shake the stimulated hair cells from their foundations, causing localized deafness. Finally, injury to the auditory nerve or to the cerebral cortex may also result in some form of deafness. The auditory mechanism consists of many interdependent parts, all essential to normal hearing.

Taste and Smell

Investigation of the sense of taste from a gourmet's viewpoint has been pursued with enthusiasm for countless centuries, but its investigation from a scientific viewpoint has been rather neglected. The sensation of taste arises from the stimulation of taste buds by soluble molecules in food. In eating, taste is intimately linked with smell, but the receptors for each are distinct in structure and location. Taste

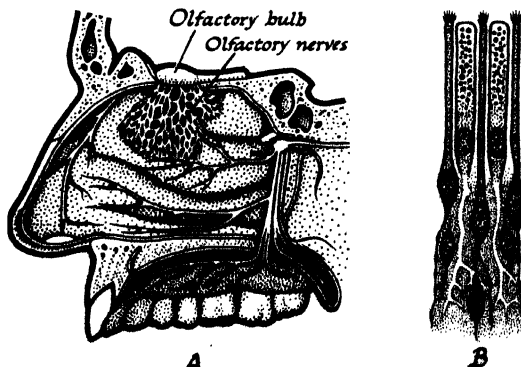
receptors are specialized epithelial structures, and differ markedly from the primitive free nerve endings of the olfactory receptors.

Taste. Taste receptors, or taste-buds, are onion-shaped groups of hair-cells recessed in the tongue, the lining of the mouth, the pharynx, and the larynx (Fig. 477). A short hair projects from each hair-cell into the recess. Like other epithelial cells, the taste cells are continually replaced by new ones, and while the severing of their nerve connection results in degeneration, they reappear when the nerve regenerates. The total number of taste buds declines with age. Not all of them have the same function, although they appear to be alike in form. Some respond to sweet, some to salt, others to sour, and a fourth group to bitter substances. They are clustered in groups according to type, thus giving the tongue regions of different taste sensitivity. The tip of the tongue is sensitive to all four tastes, but especially to sweet and salt. Sour perception is localized along the lateral margins, while perception of bitterness is most acute on the upper surface of the back of the tongue.

The value of taste as a guide to the selection of an adequate diet is suggested by experiments on rats with severed taste nerves. Offered solutions with and without essential vitamins, normal rats appear to choose reasonably well, whereas those deprived of taste do not.

Smell. Although the sense of smell is much more versatile than taste, the basic smells that can be perceived are limited in number. It is generally considered that smell is a direct response to volatile molecules that land on the

Fig. 478. A. Section through the nose showing olfactory bulb and nerves. B. Olfactory cells in the nasal mucous membrane.



ends of the olfactory receptors. A recent theory suggests that smell may be a modified visual sense. Certain experiments with bees suggest that infra-red rays, given off by the body, are differentially reflected from certain objects or substances, impinge upon the nasal membrane, and thus give rise to smell.

In some animals an acute sense of smell serves as a warning of possible danger or as a tracking organ. In man, the sense is far less acute, and serves quite different functions in discriminating between foods.

Taste and smell are so closely allied in our experience that the role of smell in sampling food is often not fully appreciated — until one has a bad cold. Although man's sense of smell falls below that of many other animals in acuteness, it is still extremely delicate. As little as .0000004 mg. of mercaptan, an alcohol, in a liter of air, a concentration equivalent to about 6 ounces in a cubic mile, can be detected!

In man the sensory area for smell is very small, occupying only about 2.5 square centimeters of the extreme upper portion of the nasal cavity (Fig. 478). Hence only a small portion of the air inhaled actually passes over it. The sense organs of smell themselves indicate their primitive nature by serving both for reception and conduction. Delicate filaments from a terminal knob on the exposed end of each cell receive the stimuli, while a single nerve fiber growing from the other end of the cell conducts the impulse toward the olfactory bulb of the brain. Free nerve endings appear to serve as supplementary receptors.

Cutaneous Senses.

Numerous sensory endings in the skin keep us informed of environmental conditions. In addition to the receptors of pressure, pain, heat, and cold, the skin may have chemical receptors.

Somatic Sensations

Still other receptors are attuned to stimuli arising in the body itself, stimuli more or less constant and lacking the sharply localized character of those affecting other senses. These are generally controlled by the lower brain centers, and only infrequently do we become conscious

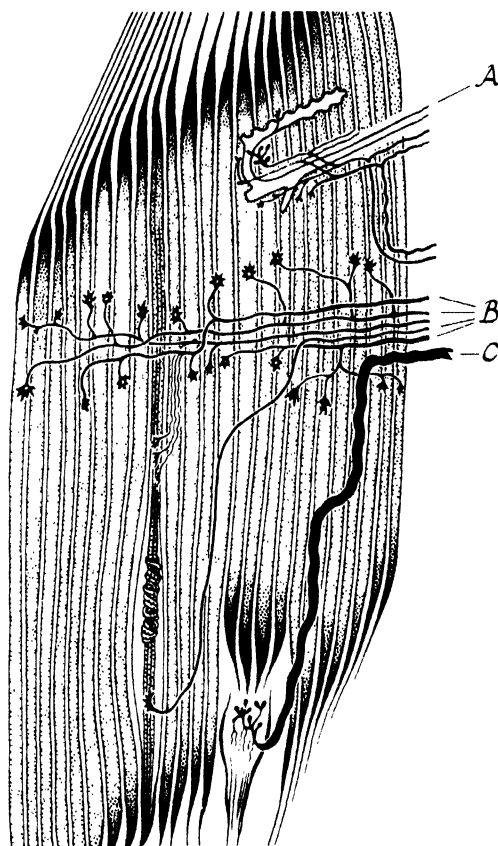


Fig. 479. Proprioceptors in a muscle. A. Blood vessel with sympathetic and pain fibers. B. Motor fibers. C. Proprioceptor fiber from tendon.

of them. But their failure leaves us insecure.

The Kinesthetic Sense. Many kinesthetic sensations (Gr. *kinein* = move + *aisthesia* = perception) arising in the muscles, tendons, and joints may not reach the level of consciousness. Yet complex nerve endings in the muscle fibers and between the ends of muscle bundles (Fig. 479) give us our sense of movement and a general awareness of the whereabouts of our various body parts, and help us to use our bodies effectively. In certain forms of syphilis, the dorsal columns of the cord carrying the sensory stimuli from the kinesthetic receptors to the brain become damaged, thus depriving the sufferer of their messages. Persons in this condition are unsure of the position of their feet and walk uncertainly, with feet thrown out and

eyes fixed upon them for some slight control.

Visceral Sensations. Certain visceral sensations such as hunger pangs and fullness of the bladder or colon can be very acute, and whereas other visceral activities, such as the movements of the intestines in digestion, never reach the level of consciousness, visceral pain sensations are well known. Oddly, the viscera were once thought insensitive to pain since they could be cut, crushed and generally mistreated during abdominal operations, yet without pain. But we know now that these stimuli were simply not of the right sort. The viscera are not normally exposed to such stimuli, and no selective mechanism has operated to evolve receptors for them. However, sensations of pain upon distention or stretching are clearly of selective value, and are present. The mechanisms of visceral sensation are very complex, and are partly regulated by the somatic nervous system and partly by the two branches of the autonomic, the sympathetic and the parasympathetic.

Organs of Balance. Parts of the inner ear not related to hearing are the organs of balance and position, namely, the *semicircular canals*, the *utricle*, and the *sacculle* (Fig. 480). The mechanism is as simple as it is efficient. Its principle, similar to that of the statocysts of a lobster or crayfish, is based upon the mass and inertia of particles within a chamber lined with sensitive hairs. Actually there appear to be two types of apparatus here — sacculle and utricle indicating static position, and semicircular canals detecting changes in position.

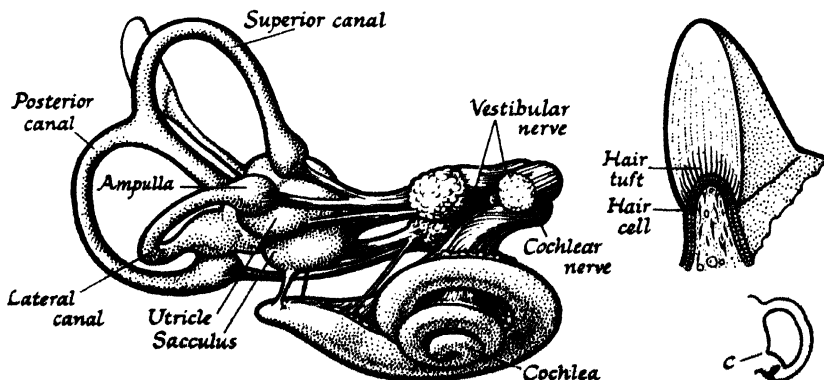
Relatively little is known about the utricle

and sacculle. They are spheroid chambers lined with hair-cells above which there is suspended a gelatinous mass. Any shift in position of the body shifts the mass, causing changes in pressure on the hair cells. A similar mechanism is found in the widened antechambers or *ampullae* at the bases of the semicircular canals. But here the inertia of the liquid in each canal bends the crista one way or another. Since there are three semicircular canals each at right angles to the others, thus representing the three planes of space, any movement will cause a current in one or more of them. The coordinating effect of this mechanism becomes clearly apparent if it is damaged, for the sufferer loses his ability to balance himself in a standing position. He may learn to balance himself reasonably well by referring to visual stimuli, but with eyes closed or in a dark room he is helpless.

REPRODUCTION

In man the basic social structure of the species as well as the life of the average individual is woven about the phenomena of reproduction. Hardly any other single factor so dominates the life of the average individual, directly and indirectly, as does the sex drive. Indeed, it has been suggested that modern civilization could not well have been achieved without it, even with asexual reproduction. Man differs from most other creatures in that his sexual drive does not markedly fluctuate with the seasons or with recurrent periods. The perennial mutual attraction between the sexes in the human species has encouraged the establishment of permanent unions, and such

Fig. 480. Left: The human labyrinth. Right, above: Diagram of the crista. Right, below: Semicircular canal with crista, showing position in ampulla.



units in turn have made it possible to rear offspring through periods of dependency of unprecedented length. Since there appears to be a relationship between the length of this period and the degree of intellectual development, it may be argued that primate sex habits have materially increased the chances for the evolution of a creature of intelligence.

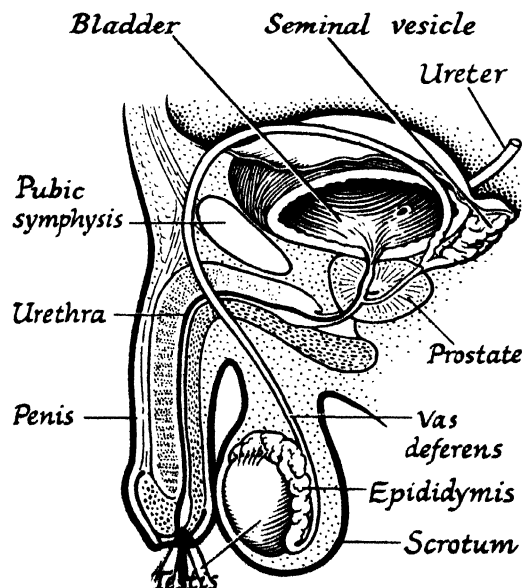
Moreover, the sex drive is deeply ingrained, like the other drives that control the behavior of living things, and its normal functioning is necessary to the successful continuation of the species. When a creature is thirsty, it drinks; when hungry, it eats. If it did not, it would die, and its defective constitution would pass away with it. Likewise, individuals without a normal sex drive are not likely to produce offspring, and those which produce offspring are likely to pass on to them the genetic constitution which conspired to make them parents, so that the drive tends to perpetuate itself. It is true that the taming of man, which was necessary for even the current brand of civilization to exist, demanded a progressive modification of instinctive behavior. That this has been possible at all, even to a limited degree, is a remarkable tribute to man's intellectual capacity. At the opposite extreme, the intellect may rebel against the tyranny and apparent irrationality of biological urges. Recognition of any urge as normal places us in the advantageous position of being able to face it and regulate it to fit the needs of society.

The Male System

While such traits as angularity in the male and roundness in the female are connected with sex, these and many others are secondary. The primary sex characteristics are those of the organs of the reproductive system. In the male these consist of the testes, sperm ducts, associated glands, and penis (Fig. 481). About a month before birth, the testes, the male gonads, descend from their primitive position in the abdominal cavity just below the kidneys into a sac, the scrotum, thus coming to lie outside the body cavity. This position appears to be essential to their normal functioning, for when

testes fail to descend, due to hormonal deficiency, or where they are artificially reintroduced into the body cavity, sperm production ceases. The higher internal body temperature is apparently responsible for this, for a slight elevation of the temperature of the testes, even when they are outside the body cavity also produces sterility. On their migration, the testes carry with them a portion of the abdominal lining, the *peritoneum*, as they push between the abdominal muscle layers through an opening called the *inguinal canal*. They also carry with them those mesonephric tubules which have become the *vasa efferentia*, and which now serve only to collect the sperm cells from the seminiferous tubules. These ducts form a dense cluster, the *epididymis*, along the dorsal and lateral margin of the testis. They then fuse to form a long single duct, the *vas deferens*, which leads back into the body cavity and joins the urethra at the base of the bladder. The *prostate gland*, about the size of a horse chestnut, surrounds the urethra at this point. Secretions of the prostate gland contribute to the seminal fluid. Hormonal changes associated with age sometimes cause it to enlarge, obstructing the urethral canal. It is also extremely susceptible to cancer. Just above the prostate gland and attached to the seminal duct, two tortuous pouches with much folded walls, the *seminal*

Fig. 481. The reproductive system of the human male.



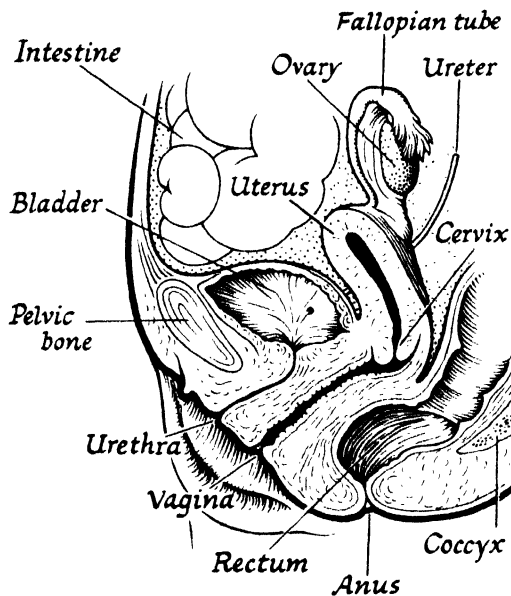


Fig. 482. The reproductive system of the human female.

vesicles, enter the urethra. At one time thought to serve for storage of sperm, these are now known to contribute to the seminal fluid substances that activate the previously quiescent sperm cells. Below the prostate and emptying into the urethra lie the *bulbo-urethral glands* (*Cowper's glands*), secreting a clear, viscid fluid.

Sperm cells are produced continuously from adolescence to advanced old age. Production of living sperm cells by men over 90 years of age has been reported. The sperm is periodically ejected, mixed with the secretions of the seminal vesicles, the prostate gland, and the bulbo-urethral glands. Under erotic stimulation, the fluid is propelled by peristaltic contractions of the seminal duct and ejaculated through muscular contractions of the urethra.

One cc. of seminal fluid contains the enormous number of approximately 70 million sperm cells, and since between three and five cc. of fluid are released at one time, the number available to a single egg is over 200 million.

Since the urethra serves both as urinary and reproductive duct, it pierces the copulatory organ, the penis. Three masses of spongy vascular tissue form the body of this organ, and reflex coordination produces damming of the

veins which carry blood away from the cavernous tissue. Distention thus provides the firmness essential to functioning of the organ.

Normal development and functioning of the male reproductive system is largely under the control of the endocrine system, especially the pituitary and adrenal glands, and the testes themselves. The latter produce *testosterone*, a hormone essential to the development of normal secondary sex characteristics, such as male voice, muscular development.

The Female System

Considerably more complex than the male reproductive system, both anatomically and physiologically, the female system consists of ovaries, oviducts or Fallopian tubes, uterus, vagina, and accessory glands (Fig. 482).

The Ovaries. The ovaries normally remain in their primitive position within the body cavity, attached to its dorsal wall near the kidneys. Each ovary is about two inches long and contains many thousands of potential ova. It is covered by a germinal epithelium, which surrounds a solid mass of modified connective tissue interspersed with an extensive network of blood vessels, and, of course, the follicles, each containing an immature egg cell.

Contrary to earlier assumptions, the germinal epithelium appears to produce new ova until about the period of birth. Many of these begin to develop but few ever mature. When an ovum, within its surrounding envelope or follicle of protective cells, actually matures, the follicle bursts, discharging the ovum still wrapped by an envelope of "nurse cells." The remaining follicle cells, always active as hormone producers, step up their endocrine activity and apparently check the further development of immature ova. Soon they change in appearance, and form a structure called the *corpus luteum* (see page 415). A single ovary may contain many thousands of partially developed or degenerating ova at any one time, all of which are or have been contributing to the normal hormone balance.

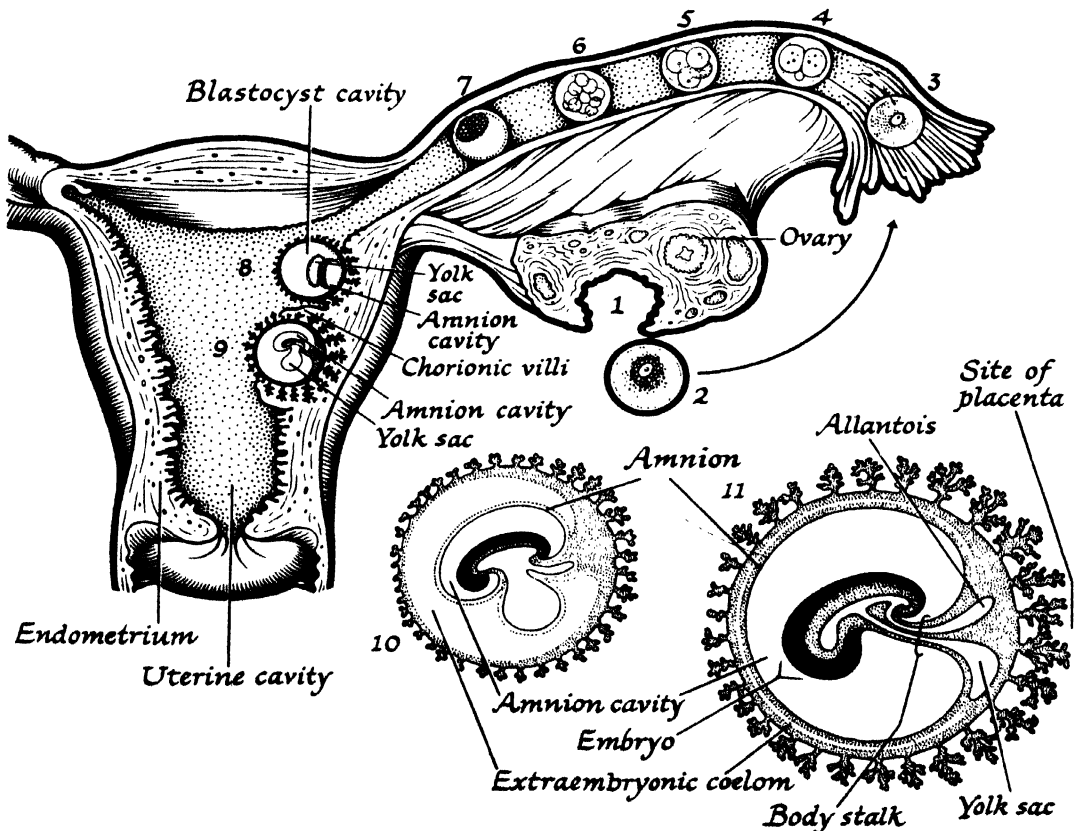
The Fallopian Tubes. The discharged ovum is swept into the funnel-like opening of the

tubular oviduct, aided by the action of the cilia which line it. It is within this Fallopian tube that fertilization normally occurs. During its journey down the tube, which probably consumes about three days, the fertilized egg undergoes its initial cleavage divisions, arriving in the uterus as an early embryo, still, however, no larger than it was when released, for no nutrients have been absorbed.

The Uterus. The uterus is a muscular, hollow organ with its lower end tapering toward the opening into the vagina. The two openings of the Fallopian tubes into it are minute. During pregnancy the lining of the uterus undergoes changes, controlled by the hormone *estrone* which the ripening follicle produces. Further changes, such as dilation, increased secretion, and accumulation of glycogen, occur under the influence of the hormone *progesterone*, produced

by the corpus luteum. For a further period of six days — nine since ovulation — the young embryo lies free in the uterus, but at the end of that period imbeds itself in the uterine tissue. The uterine epithelium proliferates around it in response to this stimulus, finally completely covering the embryo, which a few days later is firmly anchored by means of root-like villi growing from its surface. By halting further ovulation, the persistence of the corpus luteum under the influences of the implanted embryo inhibits the periodic uterine changes involved in menstruation. The increase in the sex hormones in the blood stream of the mother soon amounts to enough to be detectable, so that pregnancy tests become possible. Injection of the urine which bears these substances into a virgin rabbit or a female of the South African toad *Xenopus* will cause them to ovulate.

Fig. 483. Implantation and development of the human embryo (diagrammatic). 1. Corpus luteum in burst follicle. 2. Newly discharged ovum. 3. Freshly fertilized ovum still surrounded by sperm cells. 4. Two cell stage. 5. Four cell stage. 6. Morula stage. 7. Blastocyst showing inner cell mass. 8. Embryo developing within chorion, showing chorionic villi. 9. Implantation. 10. Later stage showing increasing size of villi at site of future placenta. 11. Further development of placenta and umbilical cord.



More recently it has been learned that an embryonic ovary transplanted into the anterior chamber of the eye of a guinea pig gives a more rapid and certain answer. Urine of a pregnant female will cause visible ovulation in the transplant within eight hours.

The Vagina and External Genitalia. The vagina, the terminal end of the female reproductive tract, is a muscular, elastic tube, serving for the reception of seminal fluid. It is distensible because the fetus must pass through it during birth. The external genitals comprise the vestibule, a depression bordered by two pairs of folds or lips, and the clitoris. The urethra opens separately into the vestibule, just posterior to the clitoris. A fold of mucous membrane, the *hymen*, usually forms a restricting margin around the vaginal opening. Glands located on the margins of the vagina produce lubricating secretions.

Ovulation

The discharged human ovum is thought to have a viability of only about twenty-four hours if it is not fertilized. Subsequent disintegration of the corpus luteum leads to reduction in the quantity of its hormones, whereupon certain pituitary hormones induce a reduction in uterine blood supply, causing the uterine epithelium to slough off, accompanied by some hemorrhage. This is menstruation (see pages 413-415).

EMBRYOLOGY

Cleavage and Early Embryonic Growth

After the human ovum has been fertilized, it undergoes cleavage, presumably much like that of other mammals, which all show considerable resemblances in their earlier stages. After these stages some differentiation is visible, and a denser cluster of cells at one pole represents the beginning of the embryo proper, while the rest of the hollow sphere is destined to form the outer embryonic membrane (Fig. 483). During the eight or nine days of this development, the embryo has been moving down the tube and into the uterine cavity.

Unlike most other amniotes, in which the

amnion is formed by an overgrowing fold (see page 470), in man a peripheral layer of cells simply splits away from those below to form the amnion, while the innermost cells similarly form the first endoderm and the vestigial yolk sac, which never contains any yolk, but may persist because it is the first center of blood formation.

The outer wall of the embryo has expanded to form the outermost embryonic membrane or chorion, mesodermal tissue has formed a lining for it, and functioning chorionic villi have grown out from it into the maternal tissues. The villi destroy the uterine tissues locally and tap vessel after vessel to form the lakes of blood which bathe them and from which they absorb nutrients. The amnion, now covered by an outer adhering layer of mesoderm, expands and eventually comes to lie close to the chorion. The enlarged cavity inside the amnion is lined on all sides with ectodermal tissue, and becomes filled with *amniotic fluid* in which the embryo floats, unhindered and well protected, at the end of the body stalk which attaches it to the chorion. The stubby body stalk elongates, and a new blind sac, the embryonic bladder or allantois, grows out from the intestine and down into the body stalk. Blood vessels and blood develop in the embryo, in the villi, and in the allantois within the body stalk, forming a connected embryonic vascular system. The expanding amnion pushes the yolk sac against the elongated body stalk, and this, degenerate yolk sac, allantoic stalk, accompanying blood vessels, and all, becomes the *umbilical cord*. The chorion with its villi unites with the adjacent mucous lining of the uterus to form the characteristic and all-important organ of exchange, the *placenta*. Like the yolk sac, the allantois degenerates and only supplies the blood vessels for the umbilical cord and placenta.

During all these general changes, the typical vertebrate pattern of organ formation has been proceeding. The neural groove appears and forms the hollow neural tube with its anterior brain swellings. The primitive endodermal cavity becomes tubular and eventually pinches off from the useless yolk sac. Sac-like protrusions from it form lungs, liver, and pancreas.

Cords of mesenchyme cells differentiate into blood vessels with enclosed blood, and in the fourth week the heart is formed and beating. Somites appear one by one, and give the embryo its primitive, segmented wormlike appearance. Pronephros, mesonephros, and metanephros follow each other in ancient traditional order. Gill pouches appear, and then disappear, and branchial arches are diverted from their pointless start toward gill supports to assume new functions as cartilage supports for mouth and roof structures, and to contribute to the bone formation of the middle ear. As appendages appear, new muscles fan out and gradually obscure the basic metameric plan. The organism is in a constant structural flux under the successive actions and interactions of the delicate chemical balance by which the genes direct the course of organization.

Later Embryonic Growth

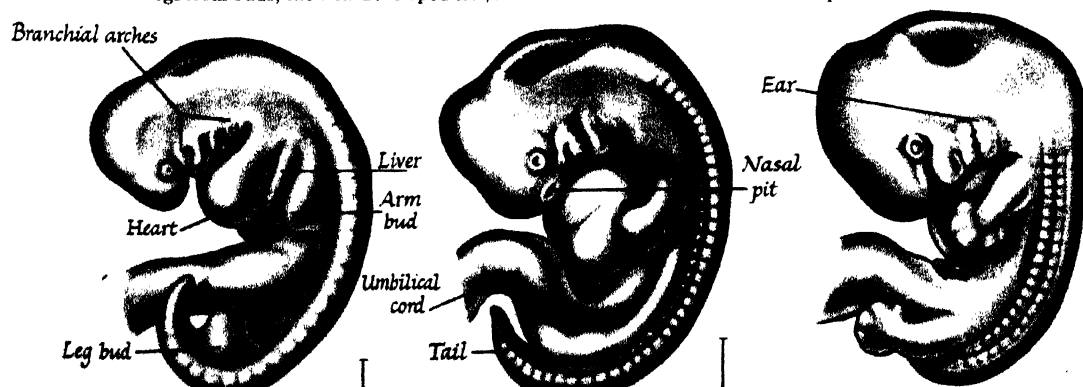
At the point where the embryo becomes implanted, the lining of the uterus changes under its influence. That part penetrated by the chorionic villi first sinks and then becomes a part of the placenta. The outer portion of it, growing over the chorionic sac, is at first vascular. This covering gradually becomes thinner and loses its vascular structure as the embryonic vesicle enlarges and protrudes from the uterine surface into the cavity of the organ (Fig. 483). As the embryo grows, the uterine cavity around it becomes smaller and eventually disappears as the covering sheath fuses with the opposite wall of the uterus.

During these membrane changes, the fetus

has been displaying intense growth (Fig. 484). At the end of the eighth week it has reached a length of almost one inch and a weight of one gram, an increase of about 2,000,000 times its original mass. Despite its minuteness, it is now a recognizable human being, though body proportions are far from final. The head represents half the entire length. Eyes are far at the side of the head, the nose is flat, and the mouth large. There is a row of nipples, and the short feeble legs would be quite inadequate for support. Circulation is well established, and the heart has been beating since the fourth week. The muscular system has progressed so that the fetus is capable of some movement, and the first signs of ossification appear in the skeleton. Testis and ovary are recognizable, although it will be another month before sex can be distinguished by any external signs. Gone are those primitive structures that gave the early embryo its peculiar inhuman appearance — the pharyngeal pouches and the prominent somites, the bulging external heart and the large tail. These have disappeared, reformed, and been reshaped.

Conditions of respiration and nutrition are quite different before and after birth. For the fetus, the placenta supplies food and oxygen, and also functions as an excretory organ, and the circulatory system must be suited to this situation. Digestive tract, lungs, and kidneys are not operative, or but slightly so, although the liver is functional. The blood is shunted away from the inactive organs and to those that function (Fig. 485). In addition to the blood vessels of the adult circulatory system there are the two umbilical arteries and one

Fig. 484. Human embryos at four, five, and six weeks of age. Development of arms and legs from buds, the well-developed tail, and the branchial arches are items of special interest.



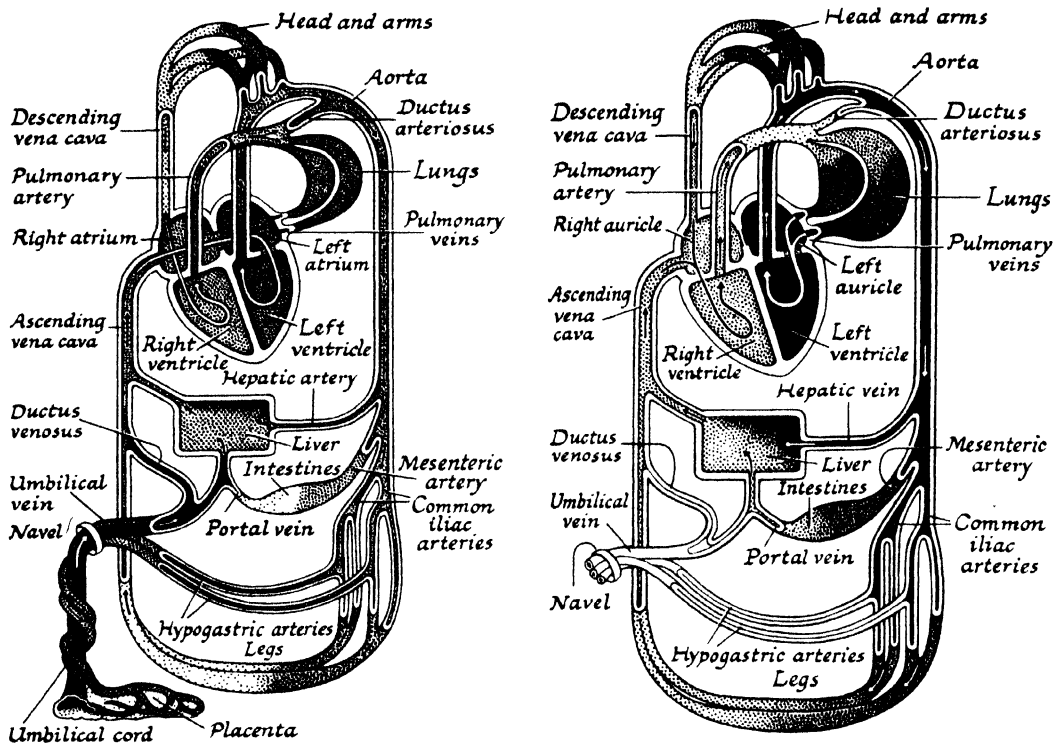


Fig. 485. Fetal circulation (left) and changes in the system which take place after birth. Depth of shading is proportional to the degree of oxygenation.

umbilical vein, passing to the capillary system of the placenta. From this organ, blood enriched with oxygen and food, and cleansed of its wastes, returns primarily to the liver.

While the outlines of the completed infant are well established at the eighth week of a human life, an incredible amount of activity remains for the eight lunar months that follow. The weight will increase 4000 times more during this period, so that at birth the child will have six to eight billion times the mass it had at conception. The organs will gradually assume their final structure and complexity: the retina will become layered and light-receptive, taste buds will form, the ear will become functional, and glands will begin their secretion, one by one. Most organs are ready to function before called upon to do so.

Parturition

At the end of the tenth lunar month the placenta begins to show signs of regression or degeneration. The mother's hormonal balance changes and under pituitary influence, the

smooth muscles of the uterine wall begin contracting rhythmically and with a quickening tempo. Labor commences, and the fetus, head first, is gradually pushed into the lower pelvic cavity. Slowly the cervix, or neck, of the uterus dilates; the soft, unfused cranial bones of the infant yield and suffer temporary displacement; and the child is born. The sharp change in environment from the uniform warmth and fluid surrounding of the uterus and amniotic cavity to the harshness of the outer world stimulates the infant to express its disapproval. By reflex action the breathing muscles contract, air rushes into the lungs, and the infant voices its first cry. Pulmonary circulation is initiated as the placental source of oxygen is cut off. The umbilical cord is cut and tied, and the stump eventually shrivels and disappears leaving the navel as a scar. The new organism is now physically independent. Placenta and umbilical cord are expelled some time later, and the uterus begins to repair itself.

Truly the body of man is "fearfully and wonderfully made."

PART SEVEN

**THE BRIDGING OF YESTERDAY,
TODAY, AND TOMORROW**





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Much of what is now known about heredity has been learned from the tiny fruit fly, Drosophila, and one of the most studied of its mutant traits is eye color. The specimen at the right has the red eye of the normal fly; at left is a mutant sepia eye; and at top is a white eye, the first Drosophila mutation discovered by geneticists.



The Physical Basis of Heredity

Over the slender bridge of the genes one generation is connected to the next, and the yesterdays reach into the present, and the present into tomorrow, as long as life shall endure. The minuteness of the hereditary link between one generation and the next is such as to challenge the imagination. It is difficult to comprehend that the genetic link between the present generation of man and the next represents a *total mass* equivalent to just one and a half drops! This is the volume of the nuclear material involved in the production of two billion human beings, with all their potentialities and differences. The way in which this microscopic stream of germ plasma is organized and handed on, and the way in which the mechanics of heredity produces the inexhaustible variety of individuals within a species, will be traced in this chapter.

Human beings with their independence and their well developed personalities make poor subjects for experiment. Most of what we know about the science of genetics has perforce been derived from the study of animals and plants. Thus in our survey of the physical basis of heredity, most of our evidence will be derived from such studies.

Genes and Chromosomes

We have already seen something of the genes. Our problem here is their behavior as units and as combinations of units during the process of transmission from one generation to the next.

Genes are remarkably stable. It has been estimated that the mean life span of a gene is 100,000 years! Yet they do mutate, and by so doing make possible evolution by natural selection. We have witnessed the amazing adaptive results of evolution, and the working principles

have been recognized: namely, the random nature of mutations and the dependence of genes on each other and on environmental conditions. But few characteristics may be traced to a single gene only, and no gene can operate in an environmental vacuum. Nevertheless, under reasonably constant environmental conditions, the effects of genes, singly and in groups, are sufficiently specific to make possible an orderly technique of purposeful breeding and a prediction of outcome that has produced startling results and holds almost unlimited promise for the future.

Hereditary variations may come about in a number of ways. Their primary source is mutation. Second, since genes lie in a specific relationship to one another in the chromosomes, disruption of normal sequences may produce visible hereditary changes. Third, new diploid combinations of genes result when two haploid gametes from unrelated lines unite in sexual reproduction. Fourth, the selection of haploid from diploid sets of chromosomes, in the formation of mature reproductive cells (spores in plants, gametes in animals) takes place in a random fashion that shuffles and re-deals the chromosomes regardless of their ancestry. This process will be described in more detail later in this chapter. Fifth, corresponding maternal and paternal chromosomes, prior to segregating into different gametes, come together and pair in an intimate juxtaposition of corresponding parts; and while so paired, they can break and exchange strictly equivalent segments. This process, called crossing over, causes separation of genes normally linked on the same chromosome, resulting in their segregation into different gametes and greatly increases the possible kinds of gametes an individual can produce.

Finally, variations from the normal haploid-diploid relationship between gametes and zygote may produce polyploid cells with new and unexpected characteristics. In these many ways, then, partly through mutations and partly the mechanics of sexual reproductive processes, the chromosomes and genes undergo the kaleidoscopic recombinations that result in the genetic variety of life and the genetic uniqueness of the individual. Without undue instability, evolution is thus made possible.

History of Genetics

The study of heredity is known as *genetics*. While this is a young science, experiments in it began unconsciously before recorded history. The breeding of domestic animals and plants with definite purposes in mind no doubt began with their domestication, perhaps 10,000 years ago, somewhere in the latter part of the Paleolithic. Gnawed bones found in the dwelling caves of early man suggest that the dog had already become a fireside companion, probably the first animal to be domesticated. We may imagine jackal-like animals frequenting the home-sites of man, scavenging on the offal left by our none-too-tidy ancestors. Orphan pups may have been adopted into the family circle, and then, inevitably, the process of human selection began to replace natural selection. Those animals that possessed the type of intelligence necessary for cooperation and willing subjugation would have been preferred, would have stayed happily, and thus have produced more of their kind. Incurably wild ones would have been rejected. Only thousands of years of such selection could have produced an animal so attuned to man's character and mentality as the modern dog. Man's most ancient animal companion naturally became his closest.

In later periods here and there, other animals — sheep, goats, cattle, and horses — were incorporated into man's pattern of living, and in turn became agents which made possible the new pattern of that relatively permanent and stable communal life upon which modern civilization is based, a pattern not possible for man the hunter.

During the same period, plants also came under domestication. Once again the way this happened is conjectural, though it requires no great imagination to reconstruct the picture. It was inevitable that lost and scattered wild grain, gathered and brought to the home-site from natural stands, would have sprouted the following season. Sooner or later someone grasped the connection, and from this to a deliberate planting of the seed was not a great step. Nor could it have been such an enormous step to begin selecting seeds from plants with the most desirable features. Nature teaches over and over the statistical lesson that "like begets like," and while we have learned that this "law" is hedged with exceptions and conditions, its crude application would, over thousands of years, almost certainly lead to improvement. That this actually did happen early in man's civilized career is not conjecture, for he has left proof in his refuse heaps. Here have been found grains markedly different from any known to have grown wild, products of selective breeding by man — ancient products of his crude genetics.

The thousands of years that followed showed little progress in real understanding of the nature of heredity. And in Europe, after the fall of the Roman Empire, much of the progress that had been made appears to have been lost. Warfare, lawlessness, and chaos well-nigh destroyed the incentive to create and improve, for man found himself in no position to be discriminating. He took what he could get. Thus history tells us that for a period probably running well into the sixteenth century, natural and unconscious human selection, rather than conscious selection by man, directed the evolution of most of our now-domesticated animals. Only in the creation of heavy breeds of war horses, strong enough to carry knights in armor was notable progress made.

Early Modern Experiments. One Robert Bakewell of Dishley in England (1725-1795), though not the first to do so, was a remarkably successful pioneer in planned selective breeding of livestock. With little basic understanding of the fundamental laws of heredity, he achieved

his success by persistently and stubbornly applying the concept that like begets like, yet with full and due consideration of the phenomenon of variability. By intensive inbreeding, that is, the mating of closely related individuals or stocks — a process then frowned upon as immoral — combined with rigid selection, he raised the average weight of beeves from 370 to 800 pounds, of calves from 50 to 148 pounds, and of lambs from 18 to 50 pounds. All this he accomplished without any real understanding of the mechanism underlying heredity.

When Darwin published his *Origin of Species* in 1857, like everybody else he still lacked a full and precise knowledge of genetics. Sir Francis Galton, cousin of Charles Darwin, was inspired by his book and though by no means the first, began studies of heredity which led to important new concepts. But Galton aimed to describe heredity in gross, rather than to make the individual analysis of single hereditary characteristics which was begun at about this time by an obscure investigator in the garden of an Austrian monastery. This investigator was Gregor Mendel, Augustinian monk and prelate, who in 1864 offered the world the first correct scientific analysis of the mechanism of heredity. He offered it, but the scientific world ignored it. With increasing bitterness, Mendel could only say: "My day will come." It came, but only after his death, thirty-six years later. This happened in 1900 when three workers, DeVries in Holland, Correns in Germany, and von Tschermak in Austria, were led almost simultaneously to conclusions similar to Mendel's, and to their surprise found that their "new" discoveries had already been published. So it was barely a half century ago that modern genetics became a recognized science.

MENDEL AND HIS LAWS OF HEREDITY

The story of Mendel and the tiny, quiet monastery garden in which he experimented with peas and flowers has often been told. But the magnitude of his achievement in tracing and analyzing the hidden laws underlying the transmission of hereditary characteristics cannot be overemphasized or overadmired. Later,

in the years before Mendel's work was recognized, such men as Schneider, Bütschli, Fol, Strasburger, van Beneden, Flemming, and Hertwig — all well known and respected — ferreted out the behavior of the chromosomes during mitotic and meiotic cell divisions, and thus laid the groundwork for our present understanding of the physical basis of Mendel's findings. But to Mendel himself, the events occurring within the cell were entirely unknown. He knew nothing of chromosomes, or of the union of the nuclei of sperm and egg cells in the fertilization process, or of the independent segregation of the pairs of chromosomes in the maturation of the germ cells — and how he would have gloried in such knowledge! Yet he showed by his analysis that the bearers of heredity must behave in just that way.

The value of Mendel's contributions stems from the fresh point of view from which he attacked the complicated puzzle of hereditary transmission, coupled with an amazing combination of lucky choices. Where others had chosen to work with general features, now known to be determined by complex combinations of genes, Mendel fortunately chose to work with a plant possessing clear-cut alternative traits, each governed by a single pair of genes. Moreover, his training as a mathematician directed him to record the exact numbers of individuals of the various types produced in his crosses. Thus he obtained his now famous ratios and discovered his laws.

Mendel's Experiments

Mendel began by surveying previous work in hybridization — that is, the crossing of two pure types (species or varieties) that differ in some outstanding features. He came to the conclusion that "among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the *number of different forms* under which the offspring of hybrids appear, or to *arrange* these forms *with certainty according to their separate generations*, or *definitely to ascertain their statistical relations*." The recognition that these three things are the

prime necessities for analyzing the nature of heredity was the basis of Mendel's success. To solve his problem then took eight years of careful work.

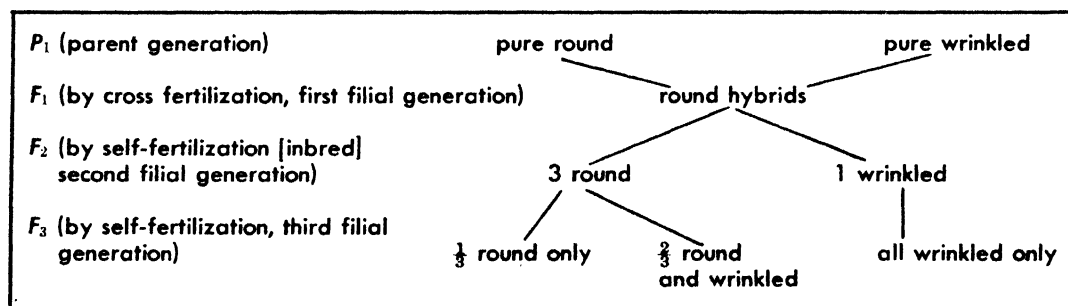
The care with which he chose the plant to work with is impressive. He demanded that his experimental organism should possess constant alternative characters; that the hybrids must during the flowering period be protected from foreign pollen, and that they and their offspring suffer no marked disturbance in fertility. Since he wished to establish statistical relations,

he observed *all* members of a series developing in each successive generation. To meet these demands he chose peas.

The thirty-four varieties available to Mendel, each pure-breeding, of course possessed many characteristics in common. These were ignored, and peas showing certain easily classified *differences* were crossed to produce hybrids. The following seven pairs of differences were selected for crossing (the characters showing dominance — later to be explained — are italicized):

1. Difference in form of the ripe seeds:	<i>round</i>	vs.	wrinkled
2. Color of stored food supply (endosperm)	<i>yellow</i>	vs.	green
3. Color of seed coat	<i>gray-brown</i>	vs.	white
4. Outer form of ripe pods	<i>simple</i> (smooth)	vs.	constricted
5. Color of unripe pods	<i>green</i>	vs.	yellow
6. Position of flowers	<i>axial</i>	vs.	terminal
7. Stem length	<i>long</i> (6-7 ft.)	vs.	short ($\frac{3}{4}$ -1 $\frac{1}{2}$ ft.)

We may diagram a typical cross, number one listed above, as follows:



Mendel united each pair of these different characters by cross fertilization and only used the most vigorous hybrids for the next cross. (The risk of false impregnation by insects was investigated and considered negligible.) Mendel found that in each of the seven crosses the character of the hybrid resembled that of *one* of the parental forms so closely that the effect of the other could not be detected at all. The character manifested¹ he termed *dominant*, and

¹ Mendel also observed the phenomenon which we call *hybrid vigor*, for in crossing long-stemmed with short-stemmed varieties, he found repeatedly that

that which seemed to disappear completely he called *recessive*.

One of Mendel's important discoveries was that the recessive trait had not actually disappeared, however, but was merely latent. For when the hybrids produced a succeeding generation (F_2) by self-fertilization, in each of the seven crosses the recessive trait *reappeared in full and unmodified form, and in a definite ratio*. Here are Mendel's actual results:

"stems 1 foot and 6 feet in length yielded without exception hybrids which varied in length between 6 feet and 7 $\frac{1}{4}$ feet."

Experiment 1	5474 round	to	1850 wrinkled
Ratio	2.96	to	1
Experiment 2	6022 yellow seeded endosperm	to	2001 green seeded endosperm
Ratio	3.01	to	1
Experiment 3	705 gray-brown seedcoats	to	224 white seedcoats
Ratio	3.15	to	1
Experiment 4	882 simple pods	to	299 constricted pods
Ratio	2.95	to	1
Experiment 5	428 green pods	to	152 yellow pods
Ratio	2.82	to	1
Experiment 6	651 axial inflorescence	to	207 terminal inflorescence
Ratio	3.14	to	1
Experiment 7	787 tall	to	277 dwarf
Ratio	2.84	to	1
The combined ratio for all seven groups is 2.98 to 1 (a very close approximation to the simple ratio 3 to 1).			

The following generation, bred from each type by self-fertilization, taught Mendel what he wanted to know about the hereditary constitution of the previous generations. Peas which showed the recessive character always bred true, that is, they never produced any other sort of offspring except those having the recessive character. But those that showed the dominant character were different: one-third of them bred true, and two-thirds yielded offspring of both kinds, some showing the recessive and others the dominant character, once again in a ratio of three dominant to one recessive. Thus, among the dominant sort there were actually two of hybrid nature to every one that was pure. The 3 : 1 ratio, based on the outward appearance (the *phenotypic* ratio) may be resolved into a 1 : 2 : 1 ratio of different genetic types (the *genotypic* ratio.)

Significance of Experiments

Now to paraphrase Mendel's analysis: Whatever hereditary factor (or factors) is responsible for the wrinkled condition of the seeds must have been present in the round-seeded hybrids, for they produced one-fourth wrinkled-seeded offspring. The latter must be genetically pure, for they produce only their own type when self-fertilized and, moreover, if a dominant factor

were present, it would mask the recessive as in the F_1 hybrids. The wrinkled-seeded plants in F_2 could only have come, then, from unions between nuclei derived from pollen grains pure for wrinkled and those from ovules pure for wrinkled. The dominant factor for round seeds must have segregated, in the formation of both pollen grains and ovules, into different cells from the factor for wrinkled seeds. In fact, exactly one half of the pollen grains of the hybrids must carry only the factor for wrinkled, and likewise exactly one-half of the ovules must bear only wrinkled, in order for them to produce by union one-fourth wrinkled ($\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$). Moreover, to produce a simple 50-50 segregation like this, only a single pair of segregating factors is required or, in fact, is possible, just as it takes a two-sided coin to give 50 per cent heads and 50 per cent tails when flipped a number of times. Thus it is possible to conclude that the hereditary difference between round seeds and wrinkled seeds depends upon a *unit* difference, upon a single pair of alternative "genes." This same conclusion holds for the other pairs of characteristics studied in peas. In these, too, each depends upon a unit difference.

To express this in general symbols, using R for the dominant unit and r for the recessive,

the hybrid is Rr . By segregation, the hybrid produces pollen grains (sperm nuclei) and ovules (ova) that are pure, being either R or r ; and half the pollen grains are of each sort, and likewise half the ovules are of each sort. Random fertilization will then lead to equal unions of R with R , R with r , r with R , and r with r . This results in $\frac{1}{4} RR$, $\frac{1}{2} Rr$, and $\frac{1}{4} rr$; or, since R is dominant over r , to 3 R : 1 r in phenotype. The ratios are thus the product of the segregation into separate germ cells of the alternative members (in modern terms, *alleles*) of each pair of unit factors (in modern terms, *genes*), followed by a random union of male with female gametes at fertilization.

This process may be shown as follows:

Hybrid parents	$Rr \times Rr$	F_1						
Gametes	$R \quad r$							
	$R \quad r$ ovules							
Pollen grains	<table border="1"> <tr> <td>R</td><td>RR</td><td>Rr</td></tr> <tr> <td>r</td><td>Rr</td><td>rr</td></tr> </table>	R	RR	Rr	r	Rr	rr	F_2 progeny
R	RR	Rr						
r	Rr	rr						

Multiple Factors

In order to see how different pairs of traits are inherited simultaneously, Mendel crossed a "round seed, yellow endosperm" $RRYY$ seed parent with a "wrinkled seed, green endosperm" $rryy$ pollen parent, producing the hybrids $RrYy$, all of which had round, yellow seeds, like the seed parent.¹

When these were selfed (self-pollinated) to produce the F_2 generation, the following results were obtained:

P_1	$RRYY$		$rryy$	
F_1	$RrYy$			
F_2	round	wrinkled	round	wrinkled
	yellow	yellow	green	green
	$RRYY$	$rrYY$	$RRyy$	$rryy$
	$RrYY$	$RrYy$	$Rryy$	
	$RRYy$			
	$RrYy$			

¹ Let R represent the gene for round seeds and r its allele for wrinkled seeds; and let Y represent the gene for yellow seeds and y its allele for green seeds.

Four sorts of seeds were obtained, showing all four possible character combinations, round yellow, wrinkled yellow, round green, and wrinkled green; the ratios were as follows:

315	round yellow	(9)
101	wrinkled yellow	(3)
108	round green	(3)
32	wrinkled green	(1)

Mendel pointed out that these figures show certain relations. First, reduced to its simplest terms, the ratio becomes very nearly 9 : 3 : 3 : 1. Furthermore, considering shape alone and ignoring color, there are 12 round to 4 wrinkled, a clear 3 : 1 ratio. Similarly, there are 12 yellow to 4 green. Clearly this new ratio is simply the numerical product of two superimposed 3 : 1 ratios. (3 round : 1 wrinkled) (3 yellow : 1 green) = 9 round yellow : 3 round green : 3 wrinkled yellow : 1 wrinkled green. In other words, *the inheritance of separate pairs of characteristics takes place quite independently*, so that the frequency of any compound type is simply the product of the frequencies of its components. For example, if wrinkled seeds occur $\frac{1}{4}$ of the time, and green seeds occur $\frac{1}{4}$ of the time, then seeds that are wrinkled and also green will form $\frac{1}{16}$ (i.e., $\frac{1}{4} \times \frac{1}{4}$) of all the seeds. This means that each hybrid parent must produce gametes of four sorts, RY , Ry , rY , and ry , in equal proportions. For the $rryy$ (wrinkled green) seeds can only come from a union of a sperm carrying ry with an egg also carrying ry ; and since the wrinkled green seeds are $\frac{1}{16}$ of the total, the gametes forming such seeds must in each parent constitute $\frac{1}{4}$ of the total, as $\frac{1}{4} \times \frac{1}{4} = \frac{1}{16}$. Figure 486 shows how the other types obtained are also formed in the correct proportions, if each parent produces the four sorts of gametes in equal proportions. We may sum up as follows: *Each pair of genes segregates independently of every other pair*. We call this *the law of independent assortment*.

Six Fundamental Laws

With the inclusion of this last law, the six fundamental principles operative in Mendel's hybridizing experiments can be stated (see also Fig. 487):

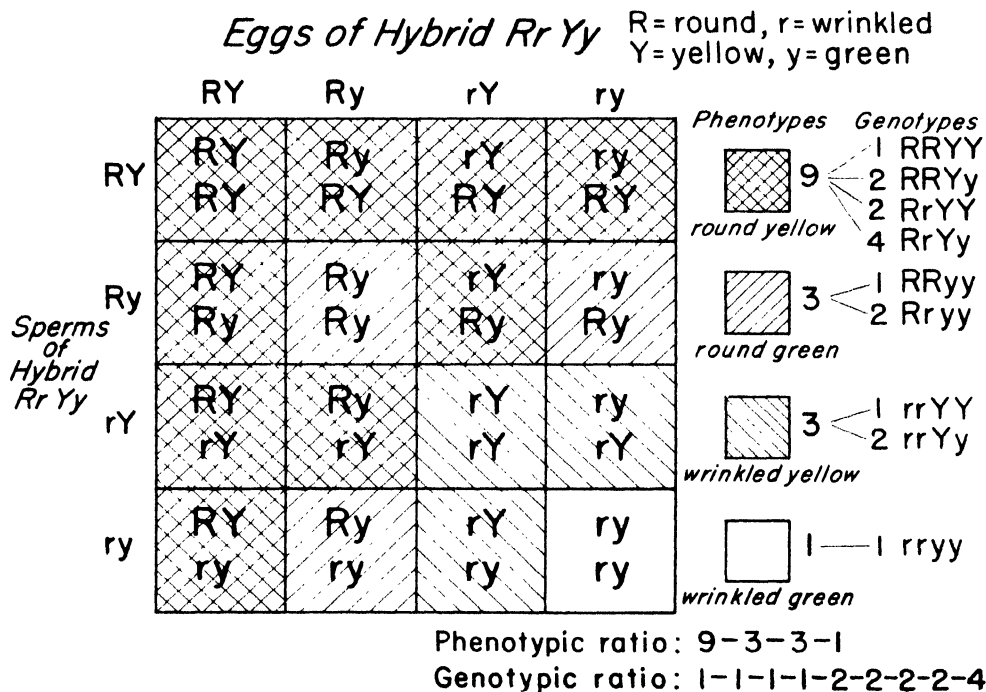


Fig. 486. Heredity of seed texture and color in peas. Letters across the top of the chart represent the genotypes of the four different kinds of eggs produced by the hybrid. Letters down the left side of the chart represent the same four genotypes in the sperms of the hybrid. Cross-hatching identifies similar phenotypes. Like genotypes are added at the right of the chart, and grouped into phenotypes.

1. The *unit character* of the hereditary determiners. This is expressed by representing the gene for each character by a single and separate letter. An organism can transmit only *whole* genes — never a portion of one.

2. The *purity of the genes*. This is expressed by the unchanging character of each determiner, as shown by the fact that no letter symbol is modified as a result of association with another. Genes never mix.

3. The principle of *dominance* and *recessiveness*. This is expressed by the choice of large and small letters for each pair of genes, as *R* and *r*, and the indication (by crosshatching) that an individual carrying either one dominant or two shows only that character, and not the recessive.

4. *Segregation* of genes prior to the maturation of the gametes. No gamete has more than one gene from a given pair. The allelic genes *Rr* of the hybrid are separated during gametogenesis.

5. *Random fertilization* of all types of egg

cells by all types of sperms. This results in offspring with their genes in pairs.

6. *Independent assortment* of different pairs of traits. One member of a pair of genes assorts at random with either member of another pair. Thus *R* may go to the same gamete with either *Y* or *y*, pure chance determining which.

The Continuity and Isolation of the Germ Plasm

In 1892, just a few years before Mendel's work was rediscovered and confirmed, August Weismann offered some ingenious postulates to explain the mechanism of inheritance. The behavior of chromosomes in cell division and meiosis was now partially known, though the hereditary significance of the chromosomes was still obscure. It had been discovered that the mature gametes contain only half as many chromosomes as were to be found in the normal body cell of the same plant or animal, and that the reduction in number occurs during meiosis. Weismann's postulates are an interesting mixture of accurate prediction and erroneous con-

clusion, but on the whole certainly demand our respect.

Weismann argued that the basis of all life is the germ plasm, which contains the fundamental units of life and heredity, and that these alone are capable of growth and reproduction. From the germ cells, he thought, all the necessary determiners are parceled out to the somatic or body cells which they produce. Germ cells produce more germ cells, whereas somatic cells can produce only more somatic cells. Thus he pictured the germ plasm as the vital stream of life flowing from each generation to the next, while he considered the body cells as mere transient by-products of the germ plasm. This is the theory of the Continuity of the Germ Plasm. Moreover, thought Weismann, changes that occurred in the somatic or body cells could not be transferred to the germ cells and hence could not be passed on to future generations. Only changes in the germ cells themselves could be inherited. This is the principle of the Isolation of the Germ Plasm.

Upon the strength of these principles, the Lamarckian doctrine that the effects of use and disuse on the parts of the body can modify the structure of future generations — in other words, that acquired characters can be inherited — was rejected. These ideas were not generally accepted by his contemporaries, even by many scientists, including Darwin himself. But time has favored Weismann in this respect. To him, too, must go a large share of the credit for associating chromosomal events with hereditary processes. He postulated that there are two kinds of cell divisions, the commonest being equal divisions in which the mother cell divides after the chromosomes have been duplicated exactly lengthwise and separated into two identical groups, a process which had then already been observed and called mitosis. Second, he postulated a rarer type of division occurring solely in the germ line, a reduction division in which the total number of determiners is reduced by half. Since the details of meiosis were then unknown, this was but a brilliant speculation. But we must not conclude that Weismann was a miraculous genius

who was always right. In a number of other ideas he missed the mark, and even his great principles, discussed here, were far too broad and sweeping to be true. Many organisms, particularly plants, have revealed no separate, isolated germ plasm.

MODERN GENETICS

Emergence of the Chromosome Theory

Mendel had shown that it is possible to gain a working knowledge of the mechanism of heredity without benefit of any actual knowledge of genes and chromosomes. While he did not know genes, he actually dealt with their effects in the form of his assumed "factors."

When Mendel's experiments were rediscovered and confirmed in 1900, the parallels between the behavior of the Mendelian units of heredity and the behavior of the chromosomes in the recently discovered sexual processes of meiosis and fertilization were quickly noted. In the gametes the chromosomes were known to be unpaired, only one of each kind — so, according to Mendel, were the hereditary units. In the fertilized egg there is a double set of chromosomes, two of each kind, paternal and maternal respectively — just so, according to Mendel, there were in the offspring pairs of hereditary units, each pair made up of one unit derived from the father and one derived from the mother. In meiosis, the homologous chromosomes could be seen first to pair with one another and then to segregate, so that the maternal and paternal homologues of any one pair always went into different gametes — so, according to Mendel, the paired units of heredity always segregated in the reproductive cells, with the result that the gametes were "pure." Finally, different pairs of chromosomes might be seen to assort at random — and according to Mendel, the different pairs of hereditary units show independent assortment. It was obvious to conclude that the chromosomes were the bearers of the hereditary units, soon to be called genes. Thus was born the Chromosome Theory of Heredity — the theory that the chromosomes are the bearers of the genes — the demonstration and conclusive

proof of which (see page 564-567) constitutes one of the glories of American scientific achievement. Today Mendel's ratios and laws take on new meaning in the light of our knowledge of the processes of fertilization and meiosis.

Fertilization

The process of fertilization in the sexual reproduction of plants and animals has already been described (see Chapters 10 and 11). Here we are concerned only with the hereditary significance of the process. In the years from 1875 to 1887, Oskar Hertwig and Hermann Fol, two German biologists, and Eduard van Beneden, a Belgian, made independent observations which demonstrated for the first time what really goes on when an egg cell is fertilized by the sperm of a male animal. The head of the sperm cell penetrates the egg (Fol) and becomes visibly transformed into a typical nucleus, comparable to that of the mature egg cell itself (Hertwig). When the egg is mature — in many species it does not mature until after the sperm cell has entered it — the egg and sperm nuclei approach each other and unite (both Hertwig and Fol). It was shown that each nucleus (sperm and egg) bears only a single set of chromosomes, that is, only one chromosome of each sort (van Beneden). In other words, the mature gametes, the egg and sperm, are *haploid*. Upon the union of the egg and sperm nuclei, the fusion nucleus carries, of course, two sets of chromosomes, the maternal and the paternal. It now has two chromosomes of each sort and is *diploid* (van Beneden). The dual heredity of the zygote and of every cell produced from it by mitosis thus depends upon the fact that the male parent and the female parent alike endow the offspring with a set of chromosomes (van Beneden). For every maternal chromosome inherited, a corresponding (*homologous*) paternal chromosome is inherited. The parallel between the paired condition of the chromosomes and the paired condition of the Mendelian units of heredity was one of the first items of evidence to support the Chromosome Theory of Heredity. We now know that for every gene upon a maternal chromosome

there is inherited an identical or mutant allele at a corresponding position (*locus*) upon the homologous paternal chromosome. (An exception to this will be discussed in a later section, page 572.)

Fertilization in plants is essentially similar to that in animals. It is only important to note that the gametes are produced by already haploid plant forms the gametophytes (in flowering plants, the pollen tube produces the sperm nucleus, and the embryo sac produces the ovum).

Meiosis

If fertilization is important in providing the dual heredity of the offspring, its counterpart, meiosis, is even more important in its genetic consequences, for it provides the greater part of all the hereditary variety within families and populations by bringing about virtually infinite recombinations of all the different sorts of genes existing within the species. It was Weismann who first saw that, if fertilization doubles the number of chromosomes per cell, there must be some sort of reduction process, prior to the formation of gametes, to halve it again, since continued doubling would be a physical impossibility. The sexual life of a species is thus seen to be a cycle, alternating between fertilization and reduction (*meiosis*), between diploidy and haploidy.

In the years between 1890 and 1905, the postulated reduction process was found to occur in both plants and animals, and a great number of cytologists of many nationalities contributed to this discovery. In animals, reduction occurs in the maturation of the gametes, the sperms and the eggs. In plants, however, it occurs in the maturation of *spores*, reproductive cells which do not require fertilization to germinate and develop, and which consequently give rise to the alternating generation of haploid gametophytes. The process of meiosis itself is essentially the same in both animals and plants. In flowering plants, meiosis, occurring in the formation of microspores and megaspores precedes the formation of the actual gametes by only a very few cell divisions.

Meiosis

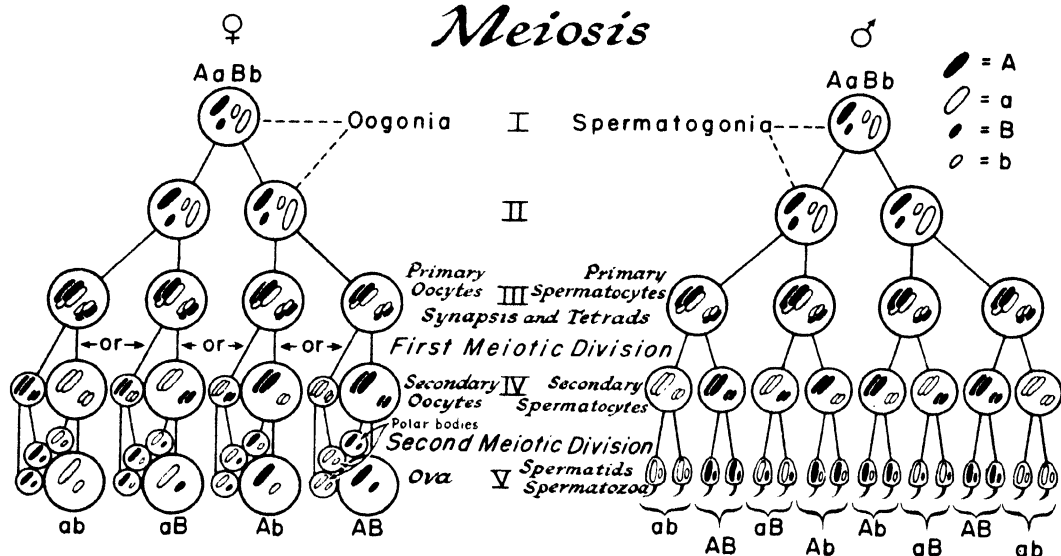


Fig. 487. Meiosis (independent assortment without crossing over) in male and female. Haploid gametes have two chromosomes each. Results of random fusion of gametes are shown in Fig. 486.

Figure 487 illustrates some of the chromosomal events during meiosis, just as Figure 486 represents the random recombinations produced in fertilization which give rise to the Mendelian ratios. In animals, the *chromosome* behavior in both sexes (with the exception of the sex chromosomes, not shown here) is identical. Only in the distribution of the cytoplasm is there a difference in the two sexes. Instead of dividing into two equal cells, in most female organisms the primary oocyte produces one large secondary oocyte and one small cell, called a polar body, which is in effect an abortive egg. In all other respects, the processes in male and female are essentially the same.

Meiosis in Animals. The primordial germ cells (I), themselves produced mitotically from the original zygote, multiply repeatedly by further mitotic divisions, producing many gonidia (II). Eventually this process comes to a halt, and a growth period ensues in these cells (not indicated in the diagram). This is more pronounced in the female, for here food storage is of paramount importance. At the end of this process, *homologous* chromosomes — that is, those containing corresponding genes or alleles — now already doubled in preparation for the ensuing division, pair closely, in geometrical

patterns, to form *tetrads*, each composed of *two pairs* of duplicate, or “twin” threads. This process, called *synapsis*, plays an important role in genic combination, for during this process homologous chromosomes may swap equivalent segments of genes (crossing-over) as we shall see later. Soon after this, the homologous chromosomes (each a twinned strand) separate from each other and segregate into separate secondary oocytes (or spermatocytes). This, it is clear, provides the mechanical basis for segregation. Furthermore, it can be seen that chance alone dictates which one of any two homologous chromosomes goes to which secondary cell. For the paired chromosomes shown in Figure 487, and consequently any paired genes located upon them, can assort in the following manner, quite independently of each other:  may yield  and , or  and . The “long” chromosome pair in no way influences the distribution of the “short,” and this provides the mechanical basis for independent assortment.

Finally the secondary oocytes and spermatocytes divide once more, *without a further chromosome duplication*, for this has already been achieved. Now the twinned strands separate, and so (ignoring crossing-over) two gen-

etically identical gametes are produced by this cell division. In the female, the unequal distribution of cytoplasm, due to the fact that the spindle lies near the surface with its axis oriented radially, again produces a large cell, the functional ovum, and a small polar body. In the meantime the first polar body may also have undergone division, making a total of three polar bodies. In the male, all four members of each quartet of cells are functional. These *spermatids*, ordinary cells in shape, pass through a metamorphosis to become mature tailed sperm cells, or spermatozoa.

Meiosis in Plants. In plants, too, only one of the quartet of cells produced by meiosis on the female side is a functional megaspore. The three other cells of the quartet fail to grow and degenerate. But on the male side, each of the four cells of a quartet of spores becomes a functional pollen grain.

In the illustration presented, the two parents were assumed to be heterozygous for two pairs of genes, carried by separate pairs of homologous chromosomes. Their genotypes are $RrYy$. Because of the segregation that takes place in meiosis, each gamete can have only one of each type of chromosome — either R or r and Y or y . This makes possible four different combinations in the gametes: RY , Ry , rY , and ry , and chance determines that they will be produced in equal numbers. Were only one pair involved, only two kinds of gametes would be possible R and y . Two pairs, however, produce combinations, as shown above. Three pairs yield 16 combinations. The number of possible combinations may be determined for any number of pairs of chromosomes by the formula 2^n , where n is the number of pairs of chromosomes. ($2^1 = 2$; $2^2 = 4$; $2^3 = 8$; etc.)¹ Since the four different kinds of gametes are produced in equal proportions, they may be given equal status in the Punnett square (Figure 486). This illustrates the product of random fusions of eggs

and sperms of four different genotypes produced by similar di-hybrid parents. The now familiar 9 : 3 : 3 : 1 ratio results.

OTHER GENETIC PROCESSES GIVING RISE TO HEREDITARY VARIATION

The mechanism of heredity thus far outlined is basically simple and essentially what Mendel deduced from his experiments. Newer discoveries of gene and chromosome behavior have made clear several additional principles which together produce an enormously complex hereditary mechanism. These principles may deal with the interactions of genes occupying corresponding loci (alleles) on homologous chromosomes or with genes occupying different loci on the same chromosome. Such interactions underlie the phenomena of *blending*, of *multiple alleles*, of *multiple effects* of single genes, and of *multiple factors*, all of which will be discussed here. Discussion of further principles which led to the establishment of the Chromosome Theory of Heredity will complete the chapter.

Blending

Though unlike alleles usually exhibit a dominance of one and a consequent recessiveness of the other, this is not always so. Frequently alleles produce a combined effect in the hybrid, a blending of their effects. Or, when one of the alleles appears to be negative in its effect, the other may reveal a stronger action when it is homozygous, that is, in a double dose, than when it is heterozygous, that is, in a single dose. This produces an apparent blending but may be only a manifestation of incomplete dominance, or an example of a cumulative effect.

The interaction of a pair of alleles to produce an intermediate characteristic may be illustrated by the crossing of white and red four o'clocks to produce pink hybrids. We may call this incomplete dominance. One dose of the gene-producing pigment gives pink, a double dose intensifies the color to red. Clearly, pinkness is a hybrid characteristic; so, instead of obtaining the 3 : 1 ratio when mating two pinks, we obtain 1 red, 2 pinks, and 1 white. Attempts to produce a pure, true-breeding

¹ There are 24 chromosome pairs in man, hence 2^{24} represents the different kinds of gametes a single individual can produce by independent assortment; and $2^{24} = 16,777,216$, — and even this does not consider crossing-over.

pink strain must obviously be futile, since "pink" is by nature hybrid. We may diagram this as follows:

		Eggs	
		R	r
Sperms	R	RR red	Rr pink
	r	Rr pink	rr white

A similar example in animals is found in the Andalusian breed of poultry. Black Andalusians crossed with white Andalusians yield only so-called blue Andalusians. These are highly prized by breeders for their color, but unfortunately they cannot be made to breed true. As with the pink four o'clocks, no matter how they are crossed, they always produce some progeny that are either blacks or whites, or some of both.

Multiple Alleles

Since most genes are capable of mutating in several, or even many, different ways, it is to be expected that different mutant forms of the same gene may exist in the population. Various pairs of alleles will exist in different individuals, and will show either a blending or a dominant-recessive relationship to one another. Thus for one single locus on a chromosome of *Drosophila* there are known to exist at least fourteen different alleles for eye color. Arranged in order of darkness of eye color, they form the following series: dark red, wine, coral, blood, eosin, cherry, apricot, buff, honey, tinged pearl, ivory, ecru, white. The wild type of eye color, dark red, is fully dominant to all the others, but any other combination of two different alleles yields an intermediate. The heterozygote between coral and white is, for example, scarcely if at all distinguishable from homozygous apricot. Any individual fly can, of course, carry no more than two members of this series of alleles.

Again, in rabbits there is a series of multiple alleles for coat color. The gene *C* is necessary

for full coat color. It has three alleles, in the following order of dominance: Chinchilla, c^{ch} , which brings about a lack of yellow in the hair; Himalayan, c^h , which produces white animals with black-tipped noses, ears, and feet; and c^a , a gene for albino. The Himalayan allele is particularly interesting, for its effects are clearly related to body temperature. It is able to produce pigment only where the temperature is lower than that normal for the body, as in the extremities mentioned. This was proved by plucking the fur from a white area of the body and then keeping that zone cold with ice while the hair was growing back in. It came in black! This shows clearly how the effects of genes may depend upon outside conditions.

Multiple Effects of Single Genes

No misconception is more widespread among those who have learned a little about Mendelian heredity than the notion that each gene controls a single character. This may be true for some genes, but certainly it is not true for most of them. Many genes produce their primary effects so early in the development of the organism that there is plenty of opportunity for the primary effect to produce secondary effects, and these keep ramifying until one is able to find many effects traceable to the same gene. An example is phenylketonuria in human beings. This simple recessive hereditary trait is marked by the inability of the body to oxidize phenylpyruvic acid so that this substance is excreted in the urine. This in itself would seem harmless enough — but we find that all phenylketonurics are imbeciles or, at best, low-grade morons. Just what the connection is between phenylpyruvic acid and intelligence no one can say at present — a fact which makes this an especially striking example of distinct effects produced by a single gene.

The most convincing proof of the multiple effects of genes comes from the study of deficiencies. Treatment with X-rays or various other potent agents may cause a chromosome to break in two places, often close together; and the piece between the two breaks may then be

lost altogether, while the two remaining ends join and heal into an apparently normal but now deficient chromosome. In this way a cell may lose certain genes, and if this happens in a germ cell, the deficiency will be inherited by subsequent generations. Deficiencies may be large or small, even to the loss of but a single gene. This may be ascertained from the cytological examination of the giant chromosomes in the salivary glands of the fruit fly, where each cross band is known to correspond to no more than one or two genes. Deficiencies of single bands, or even of fractions of bands, can be seen with the microscope. It is significant that whenever any such deficiency is made homozygous by inbreeding, the result is in practically every instance lethal. From this, it would appear that almost every gene (or at any rate a majority of the genes), is necessary to the very life of the organism — its presence is a *vital* necessity. Yet these are often the very same genes that we recognize only by some quite superficial change in character which they cause when they mutate, such as some alteration of eye color or body color, or perhaps some slight change in form or function. It becomes increasingly evident that the genes are doing many hidden things of great importance in the development and life of the organism, things of which we have as yet but little knowledge.

Multiple Factors

A blending superficially like that seen in the cross of red with white four o'clocks or of black with white Andalusian poultry occurs when white and Negro persons mate. A uniform hybrid type, the mulatto, with woolly hair but an intermediate skin color, is produced in the first generation. But when first generation mulattos mate, the segregation for skin color is not simply into the two original types plus the mulatto type, in a ratio of 1 white: 2 mulatto: 1 black.

Instead, approximately five grades of skin color occur in a ratio of 1 white : 4 light brown (brunette) : 6 mulatto : 4 dark brown (chocolate) : 1 black. As the sum of this ratio, like the 9 : 3 : 3 : 1 ratio, amounts to sixteen indi-

viduals, it is evident that two pairs of genes on separate pairs of chromosomes are responsible for the segregation. We may call these genes *Aa* and *Bb*. Since the original white and black types each segregate out in $\frac{1}{4}$ of the progeny, they must be the double homozygotes, *AABB* and *aabb*. The mulatto is *AaBb*, and like the previous dihybrid (page 553), forms four kinds of gametes, *AB*, *Ab*, *aB*, and *ab*. As the combinations of the previous Punnett square show, a cross of two dihybrids will produce $\frac{1}{16}$ with four dominant genes, $\frac{4}{16}$ with three dominant genes, $\frac{6}{16}$ with two dominant genes, $\frac{4}{16}$ with one dominant gene, and $\frac{1}{16}$ with no dominant genes.

Because of the dominance, these collect into the 9 : 3 : 3 : 1 ratio, but if, instead of dominance, we assume that *A* and *a* blend like red and white in four o'clocks, and *B* and *b* likewise; and if *A* and *B* are about equally effective in producing melanin pigment in the skin, then the 1 : 4 : 6 : 4 : 1 ratio will stand as the phenotypic ratio. In other words, one may, from the phenotype alone, deduce the number of "black" and "white" genes present in the total of four skin-color genes carried by an individual at these two loci, although one might not be able to tell at which of the two loci specific genes were carried. *AAbb* would, for example, be indistinguishable from *AaBb* or from *aaBB* in actual skin color, although they are quite different genetically, since *AAbb* and *aaBB* would each be able to produce only one sort of gamete, whereas *AaBb* can, as we have seen, produce four sorts.

One corollary of this analysis worth noting is that a mating of any person having "black" genes with a pure white cannot possibly produce offspring darker than the dark parent. But a mating of two persons each carrying one or more "black" genes can produce children darker than either parent. A complication results from the fact that persons with only one "black" gene are sufficiently light-skinned to be indistinguishable in skin color from many non-Negro individuals of the less blond white ethnic groups. A child with two Negro grandparents has a fairly good chance ($\frac{1}{16}$) of having

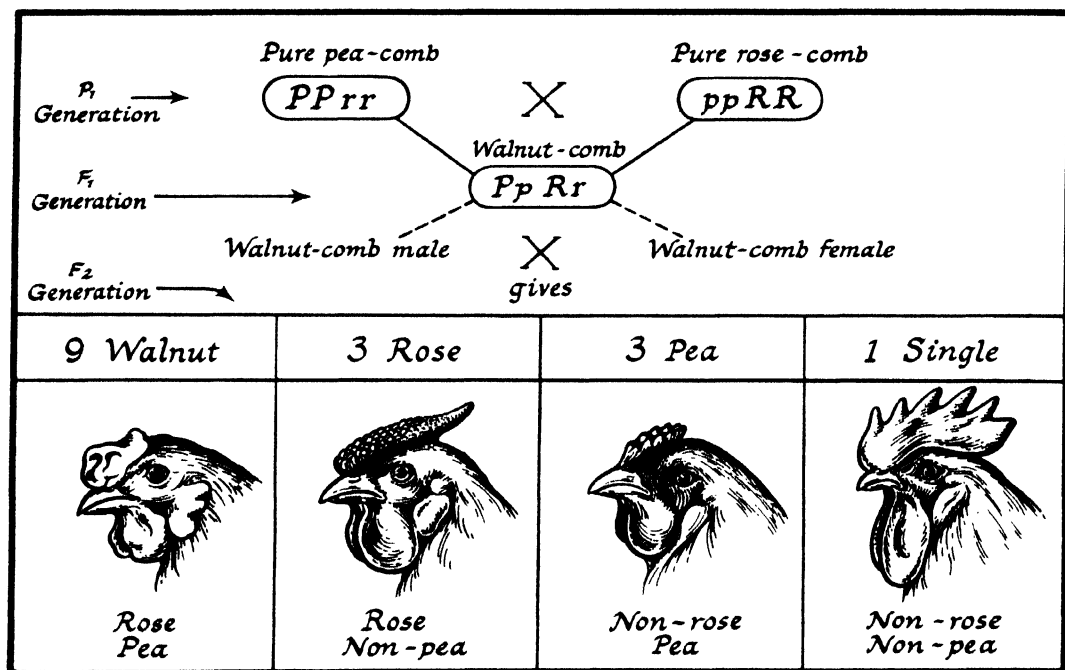


Fig. 488. Effect of supplementary genes in producing a new phenotype. A pure pea-comb fowl crossed with a pure rose-comb produces walnut comb. The F₂ generation bred from such a hybrid gives phenotypes as shown. Also see text.

no trace of dark skin color, and, it is particularly to be noted, no possibility in that case of transmitting dark skin color to later generations. Conversely, a child with two white grandparents has an equal chance of being fully black in skin color.

Of course, skin color is not the only characteristic that makes a Negro a Negro or a white a white, but the actual number of observed physical distinctions is not great, and few genes are needed to account for them — one for woolly hair, and a number for facial proportions and anatomical features. Since most of the racial characters are not distributed on an all-or-none basis, they cannot be used as sure criteria of racial origin. Thus the frequency of blood type Rh₀ is relatively high in negroes (42 per cent) and low in whites (2.5 per cent); yet many Negroes are not Rh₀, and some whites are. In short, while it is not very likely that a pure white child, phenotypically and genotypically, would result from a mating of two mulattos, it is not at all impossible. The probability is not 1 in 16, but it may not be lower than 1 in 500 or 1 in 1000. These con-

siderations point up the unsoundness of certain laws, in this country and elsewhere, that stigmatize an individual on account of a single grandparent or great-grandparent.

Supplementary Genes

Other possibilities exist for the interaction of genes carried by independent chromosomes which may produce modifications of the 9:3:3:1 ratio in F₂ generations. One of the simplest arises when the two dominant genes of the independent pairs interact to produce an altogether new phenotype. Such genes are called supplementary genes. A single example should make this clear. In chickens, besides the common crested single comb, rose combs and pea combs are known (Fig. 488). Each of these behaves as a simple dominant to single comb. But rose-combed fowls crossed with pea-combed fowls give an altogether new type of comb, called walnut. This is simply due to the combined effect of the two dominant genes, for when two walnut-combed chickens are bred together, the F₂ generation consists of 9 walnut-combed:

3 rose-combed: 3 pea-combed: 1 single-combed. The situation is exactly as in the previous 9:3:3:1 ratios discussed, with the exception that the rose comb gene together with the pea comb gene produces an individual with a walnut comb. But this is not a hybrid characteristic produced by the blending effect of two alleles, as in pink four o'clocks or Andalusian blue chickens. Here two unrelated genes in different chromosomes produce a cooperative effect. Where it was impossible to produce a pure breed of pink four o'clocks or Andalusian blues, it is quite possible to produce a true-breeding walnut-combed fowl. For some of the walnut-combed birds — one out of nine, on the average — should be *P P R R*. These, if mated together, would produce a pure breed. In order to distinguish these double homozygotes from the birds that carry only one *P* or one *R* gene, a breeder may make a *test cross*. Each bird to be tested is bred to a single-combed (double recessive) individual. Since these produce only gametes carrying *pr*, any recessive genes present in the bird being tested will show up in the offspring. A walnut combed bird heterozygous for *P* (that is, *Pp*), will produce a progeny one half of which will lack the *P* gene and so be either rose-combed or single-combed. The same principle applies to a bird heterozygous for *R*. Only the *P P R R* individual will produce solely walnut-combed offspring in the test cross, since all offspring will have one *P* and one *R*. The proven *P P R R* birds can then be mated together to start the pure breed.

Complementary Genes

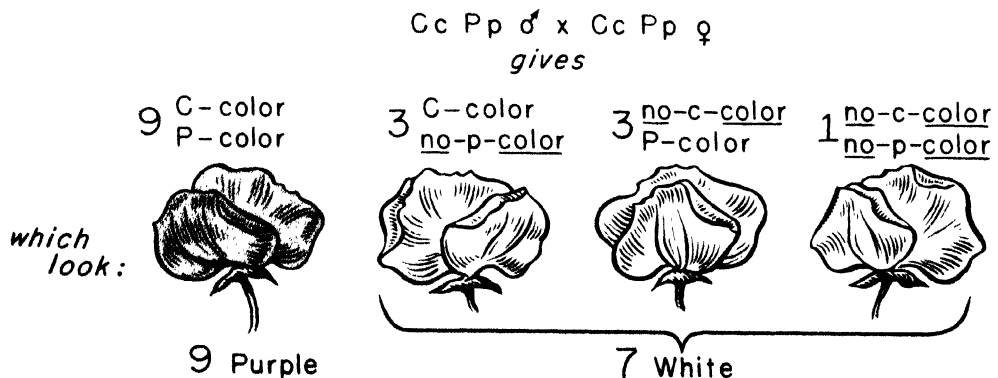
Another interaction of genes in independent chromosomes occurs when two different dominants must each be present to produce a visible effect at all. These are *complementary genes*. There are two pure strains of white sweet peas that, when crossed together, give only purple-flowered plants in the F_1 . The F_2 yields 9 purple to 7 white. Only those having at least one of each of the two different cooperating genes will be purple, while classes with either the one *or* the other of the two dominant genes will be phenotypically white, as will the double recessive (Fig. 489).

Normal hearing in man appears to depend upon complementary genes; that is there are two distinct kinds of deafness, both recessive, and normal hearing depends upon the presence of a normal dominant gene at each of the two loci.

Inhibiting Genes

Inhibitor or *suppressor* genes sometimes suppress or mask the effect of a gene in an independent chromosome. A white Leghorn chicken (*IIWW*) mated with a white Silkie (*iiww*) gives an all white F_1 (*IiWw*), and an F_2 composed of 13 white: 3 colored chickens (1 *iiWW*, 2 *iiWw*). This is because the dominant gene for white (*I*) in the White Leghorn acts as a suppressor of the dominant gene for feather color (*W*) in a different chromosome. For this there is also a recessive mutant for white (*w*), responsible for the white of the white Silkie. This example

Fig. 489. Effect of complementary genes in producing a new phenotype. Two pure white strains produce a purple pea. Inbreeding of the purple hybrid produces a 9:7 ratio of purple to white.



is particularly instructive because it shows that the same phenotype (white feathers) can be produced by different genes in the same species, and that it may in one instance be dominant and in the other recessive.

Duplicate Genes

If each of the dominant genes in the two pairs produces exactly the same effect alone, but a cumulative one when both are present together, then the ratio is shifted to 9 : 6 : 1. In Duroc-Jersey hogs there are two dominant genes either of which alone makes the hog sandy in color, while together they intensify the reddish tint to the typical red which is standard for the breed. The double recessive is white, like a Poland-China pig. These are *duplicate genes* which act cumulatively. One may also find duplicate genes which do not interact in a cumulative way, but where either alone produces the same effect as both will together. Thus of 16 F_2 individuals, 15 will have one or the other or both dominants, and all will look alike. Only the double recessive is different: hence the 15 : 1 ratio. Feathers on the shanks of chickens are inherited in this way, the plain unfeathered shanks of most breeds depending on the presence of the double recessive.

Multiple Factors in Quantitative Variation

Examples discussed up to this point have dealt primarily with qualitative traits, although some, like skin color in Negro-white crosses, begin to appear quantitative, as do height or weight or intelligence. Since the characteristics that mean most to us, those that determine our "normality," are quantitative, it is important to see whether these may also be subject to control by the genes, and if so, just what mode of heredity is involved.

Blending, as in the production of pink four o'clocks and of blue Andalusian chickens from purebred parent types, gives us a first approximation to quantitative inheritance in the ratio 1 : 2 : 1. A still better approximation is found in the 1 : 4 : 6 : 4 : 1 ratio appearing in the offspring of mulattoes. The results of a cross between two varieties differing by three such

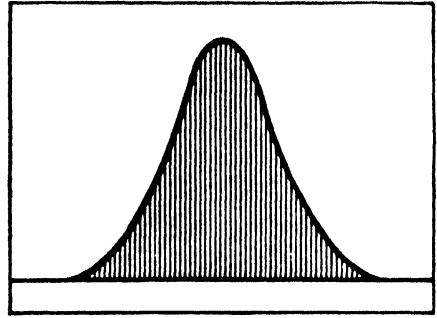


Fig. 490. The bell-shaped normal frequency curve, derived from the expansion of the binomial expression $(a + b)^{20}$, corresponding to the frequency distribution of a characteristic which is determined by ten pairs of interacting genes. (After Glass, *Genes and the Man*)

pairs of non-dominant, cumulative genes, such as those determining the difference between red-seeded and white-seeded wheat, reveal in F_2 seven distinguishable grades of color, from red to white, in the ratio 1 : 6 : 15 : 20 : 15 : 6 : 1.¹ As the number of pairs of genes determining a characteristic increases, the shape of the distribution obtained approaches more and more closely the form of the bell-shaped curve shown in Fig. 490. This curve depicts the normal probability of inheriting a quantitative trait dependent on ten or more pairs of genes. It does not, in fact, matter very much whether there is an absence of dominance in these genes or not, for if a sufficiently large number of pairs of genes is involved, it is likely that the dominant genes acting in one direction will be equalled in number by the dominant genes acting in the opposite direction. Nor is it necessary for all the pairs of genes to have the same strength of influence over the character, for strong genes in one direction will be balanced by strong genes in the opposite direction, and weak genes similarly by weak.

Coat color in rabbits is known to be determined by no less than thirteen *different* pairs

¹ Mathematically these three ratios are each an expansion of the expression $(a + b)^n$, where n is respectively 2, 4, and 6. This is the Binomial Expression which you may remember from your study of algebra in high school, and its expansion to any power forms a binomial distribution.

of genes, some linked and some on different chromosomes. At several of these thirteen loci multiple alleles exist through mutation of the original wild-type genes which have been selected by nature for their contribution to the adaptive character of coat color. These alleles may be either dominant or recessive to their respective wild-type alleles, but genes which have survived natural selection are, significantly, usually dominant, inasmuch as dominance itself gives them a higher selective value. One cannot escape noticing that the new mutants of the wild type genes usually produce effects that would be detrimental in nature, as is to be expected. The genetic formula for coat color in wild rabbits is written thus: *AABCCDD^ee^eenenDuDuVLLRRSSNNYY*. The formula emphasizes several of the facts previously stated. It indicates the complexity of the hereditary nature of such an apparently simple feature as the color of an animal's fur, and shows how few recessives enter its makeup.

Since characteristics depend not only on the interaction of many genes but also on environment, it is not strange that wide divergence occurs in populations of organisms. This whole range is "normal." When we start setting limits on either side of the average, limits beyond which we regard the individuals as abnormal, we have to be arbitrary. For such limits can be drawn at one place as well as another; and anyway, without the individuals representing the extreme deviations in both directions, the group as a whole would not be normal. In other words, it takes morons and idiots, as well as geniuses, to make a normal population, given our present assortment of genes affecting intelligence. This does not mean, of course, that with a better lot of genes we could not have a normal population with a higher average intelligence, but the genes would have to be different than they are — a better selection.

A question of considerable importance that comes up here is what will happen when various sorts of persons from such a heterogeneous F_2 marry and produce a family, for the entire human population, at least in a melting-pot

like the United States, may be regarded as essentially like such an F_2 generation. Will underweight by underweight produce only underweight children? Will genius by genius produce only geniuses? And so on. The answer is not simple, but in general runs as follows: Matings of individuals from the same extreme of a genetic distribution produce mainly offspring less extreme than the parents but between them and the mean of the entire population. Parents from the middle of the group produce offspring on the average also falling in the middle, but possibly ranging from one extreme to the other. Parents from opposite extremes tend to produce intermediates. In other words, there is a tendency for the offspring to regress from the positions in the distribution occupied by their parents toward the general average. But there are individual exceptions, due to the chance assortment of favorable or unfavorable combinations of genes through meiosis and fertilization, such that it is not inconceivable that two moron parents might have a child who ranks as a genius — or, unfortunately, the converse — it is merely highly improbable.

Most of the children of average couples will conform to the normal distribution for all such quantitative characteristics as height, weight, mentality, general vigor, temperament, and resistance to disease, in so far as these are inherited. But it must not be forgotten that the environment also causes marked variations in these characteristics, and that variation, within a relatively homogeneous group, also takes the form of a normal frequency distribution. So the bell-shaped curve does not tell us what the cause of variation is. It may be due to genetic differences; it may be due to environmental differences; or, most likely, it is due to both acting inextricably.

We must therefore seek for other evidence to make sure that such quantitative characteristics as those of which we are speaking are truly subject to genetic influence. This may be found most readily by comparing the degree of resemblance between one-egg twins, on the one hand, and two-egg twins of the same sex,

on the other, providing the members of each pair of twins have shared virtually the same environment. For the monozygotic, or one-egg twins, share all their genes in common, whereas the dizygotic twins share besides those genes for which their parents were homozygous, on the average, only one-half of those for which their parents were heterozygous. Whenever we find that monozygotic twins agree in respect to a trait considerably more often than dizygotic twins of the same sex, we can be confident that hereditary factors are of considerable importance in determining the variation of that trait in the population. For example, even though tuberculosis is a disease caused by a microorganism, and infection is necessary for tuberculosis to develop, nevertheless it is nearly three times as common among the twins of monozygotic twins who have it, as among the twins of dizygotic twins who have it. This shows that heredity plays a strong part in determining the susceptibility of individuals to the attack made upon them by the mycobacterium of tuberculosis. In general, physical characteristics show the greatest degree of concordance among one-egg twins as compared with two-egg twins; intelligence is somewhat less highly concordant; and temperamental characteristics agree only moderately better in the former group than in the latter. However, the figures in the table below should arouse considerable thought.

The last is particularly astonishing, but we must keep in mind that what is inherited is not criminality itself, but a particular genotype that in certain surroundings, under particular circumstances, leads to conduct of a socially disapproved sort. The environment is no less to blame, because the genotype is weak; and

in a better environment, the same genotype might prove itself adequate.

THE CHROMOSOME THEORY OF HEREDITY

We have said (page 555) that the Chromosome Theory of Heredity — the theory that the chromosomes are the bearers of the genes — was largely the product of the work of American geneticists. It was by the study of the exceptions to typical Mendelian patterns of inheritance that the proofs of the theory were found. "Treasure your exceptions" was the great rule in the crowded old laboratory at Columbia University where Sutton outlined the Chromosome Theory while still a graduate student, where Montgomery and Wilson worked on the sex chromosomes of insects, and where, just a few years after, Thomas Hunt Morgan started breeding the now famous little fruit-fly *Drosophila* and gathered that brilliant group of students who developed the final proofs.

Linkage and Crossing Over

The first exception was predicted by Sutton before it was ever found. The number of chromosomes in an organism is relatively small, while the number of inherited characteristics and presumably the units that determine them, is vastly greater. It must follow that, if the chromosomes are the bearers of the genes, a considerable number of genes must be contained within each chromosome. Pairs of such genes, lying in a single pair of chromosomes the two members of which segregate at meiosis, cannot assort at random according to Mendel's Law of Independent Assortment. Genes in the same chromosome cannot be transmitted independently, and genes in homologous chromosomes that always segregate will have to segregate too. Consequently each pair of chromo-

	CONCORDANCE IN MONOZYGOTIC TWINS		LIKE-SEXED DIZYGOTIC TWINS	
	NO. PRS.	PER CENT	NO. PRS.	PER CENT
Schizophrenia	41	68.0	101	15.0
Manic depressive psychosis	?	70.0	?	16.0
Tuberculosis	78	87.3	230	30.2
Criminal record	104	67.3	112	33.0

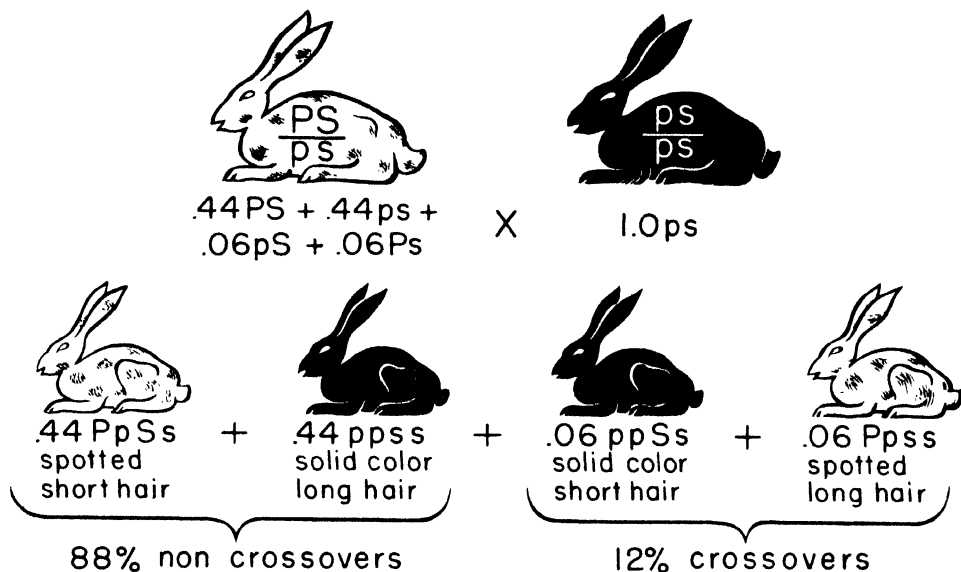


Fig. 491. The effect of crossing-over as shown in a test cross of a short-haired spotted rabbit, $XX PpSs$, with a double recessive, $ppss$ (above). This cross produces offspring (below) in the same ratio as the gametes produced by the heterozygous parent.

somes will contain a “linkage group” of pairs of genes. The number of linkage groups, Sutton predicted, must correspond in any species to the number of its pairs of chromosomes.

The first case of the predicted linkage was found by English geneticists (Bateson and Punnett) in the sweet pea three years later — a linkage between the pair of genes for purple vs. red flowers, and that for cylindrical vs. round pollen grains. The proof that the number of linkage groups equals the number of pairs of chromosomes could of course only be demonstrated after the genetics of an organism was rather thoroughly known, after years of experimental work done with it. In those organisms studied most intensively and possessing a low chromosome number the proofs are now clear. Indian corn has ten pairs of chromosomes and ten linkage groups; the sweet pea has seven of each; *Drosophila virilis*, six; *Drosophila melanogaster*, four; *Drosophila pseudo obscura* five; *Drosophila willistoni*, three; the mold *Neurospora*, seven, and so on.

If the linked genes stuck together without exception, it would be difficult to tell whether coupled characteristics are determined by different pairs of genes with distinct effects or

whether only one pair of genes with a multiple effect is responsible. Since the characteristics did occasionally show up in new combinations, it was evident that they were determined by distinct gene pairs. For example, in a cross between the purple-flowered sweet peas with cylindrical pollen grains, on the one hand, and the red-flowered round-pollened peas, on the other, the F_2 generation yields, besides the two original types, some that are purple-flowered with round pollen and some that are red-flowered with cylindrical pollen; but the original types greatly outnumber the recombinations.

A further example, using a test cross, will show more clearly what happens. In domestic rabbits a dominant gene P produces short hair, its recessive allele p , long hair; and a dominant gene S produces spotting, its recessive allele s , solid color (Fig. 491). A doubly heterozygous short-haired spotted rabbit, $PpSs$, may be crossed to a doubly homozygous $ppss$, long-haired and solid-colored rabbit. If the two dominant genes had come from the same parent of the dihybrid, and if they were inseparable or simply two different effects of the same gene, then the test cross could yield only two sorts of offspring, short-haired and spotted ($PSps$),

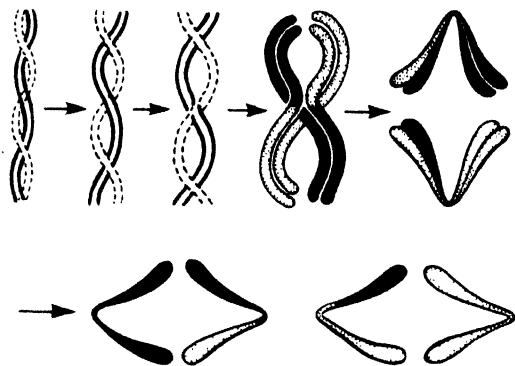


Fig. 492. How chromosomes may cross over.

and long-haired solid colored (*psps*). On the other hand, if *P* and *S* were on separate pairs of chromosomes, then by the law of Independent Assortment, four sorts of rabbits would be produced in equal numbers, namely, the two above sorts plus short-haired solid-colored (*Ppss*) and long-haired spotted (*ppSs*) ones. Actually, neither expectation is realized. All four possible sorts are produced, but not in equal numbers. The two kinds which represent the original combinations of the genes in the parents of the dihybrid, namely, the short-haired spotted and the long-haired solid-colored, together account for 88 per cent of the offspring; and the recombinations (short-haired solid-colored, and long-haired spotted, respectively) account for only 12 per cent. Thus it is clear that length of hair and type of coloration are controlled by separate pairs of genes, but it is also clear that these do not lie on separate pairs of chromosomes, since they do not recombine at random. Yet, if the two pairs of genes are carried by the same pair of chromosomes, how is it possible for them to recombine at all?

The explanation is found in a phenomenon called *crossing-over*, which is not only to be deduced from such genetic behavior as the above, but can also be observed in the chromosomes during meiosis (Fig. 492). The homologous chromosomes in synapsis, it will be recalled, are each in a duplicated state, so that a pair of synapsed chromosomes is actually made up of four threads, a tetrad composed of two pairs

of identical or "sister" strands. Just how and why the next event occurs is not known — but that it does occur can be clearly demonstrated. Two of the strands, always non-sisters, break at *exactly* corresponding levels, and then the pieces are swapped, so that after the strands are healed together again two new sorts exist, each one made up of segments derived from two originally different chromosomes. This process of crossing-over is very frequent, taking place as a rule in every pair of synapsed chromosomes and often at several levels in the same tetrad. It appears that the exchange can take place at virtually any level, and thus any two adjacent genes may become separated. The frequency of crossing-over between two gene loci in the same chromosome varies in direct proportion to the "distance" between them, that is, to the number of other genes and possible cross-over points between them.

To return to our rabbits, we can now see that the lower frequency of recombinations in the test cross, and the higher frequency of rabbits with the original combinations, are due to crossing-over. Sometimes the pair of chromosomes involved does not happen to cross over at all in the region separating the pairs of genes controlling the length of hair and type of coloration, and even when they do, only two of the four strands involved are crossovers while the other two maintain the original combinations. So the crossovers are always fewer. Since in this case they total only 12 per cent, we may speak of the two pairs of genes as fairly closely linked.

Sturtevant, one of Morgan's famous students, was able from these relations to prove that the genes are linked in linear series, like beads on a string, and then began the amazing construction of theoretical maps indicating the order of the gene loci and relative intervals between them. The reasoning is simple enough. For example, if a stick of chalk be marked with a chain of letters, *A* to *Z*, from one end to the other, and then dropped so as to break it into two or more sections, it is inevitable that *A* will become separated from *Z*. It is barely possible that *A* will even be separated from *B*,

more likely from *C*, and in increasing probability as the distance separating the letters increases. So the frequencies of crossing-over between genes are considered to be measures of their relative distances apart on the chromosome. Considering any three gene loci, it is clear that if they are arranged in a linear series, then the distance between the two more distant loci should equal the sum of the distances between each of them and the locus in between — just as the distance from Washington to New York on the railroad is the sum of the distances from Washington to Philadelphia and from Philadelphia to New York. By comparing crossover frequencies it is therefore possible to map the genes.¹ This has been done not only for hundreds of genes in the four pairs of chromosomes of the fruit fly, *Drosophila melanogaster* (Fig. 493), but similarly for genes in the ten pairs of chromosomes of maize, in the chromosomes of the chicken, of the mold *Neurospora*, and even, to a limited extent, in those of man himself.

Chromosome Rearrangements

The order of the genes determined by the method just described is the same within most organisms of a species, or at least of a local race. But sometimes an individual or a breed is found that has its genes, within a certain chromosome, arranged differently; or even has genes transferred from one chromosome to a chromosome of a different pair. Such changes are often more readily detected by looking at the chromosomes through the microscope than by studying the changes in crossing-over and linkage which are produced.

The prophase chromosomes in the meiotic divisions of pollen grains of maize are large and well paired, and any considerable differences between homologous chromosomes may be detected through the presence of loops and buckles, or of pairing of two regions of one chromosome with different chromosome partners. In 1933 it was discovered that the sali-

¹ One must, of course, take account of possible double or multiple crossovers between loci that are some distance apart.

vary glands of all dipterans — which of course fortunately included the fruit fly *Drosophila melanogaster*, whose heredity has already been so intensively studied — contain giant synapsed chromosomes a hundred or more times the length of ordinary chromosomes and thousands of times their volume (Fig. 494). Such an

Fig. 493. Map of chromosome I (X chromosome) of *Drosophila melanogaster*, showing relative positions of genes in their linear order, as derived from crossing-over frequencies.

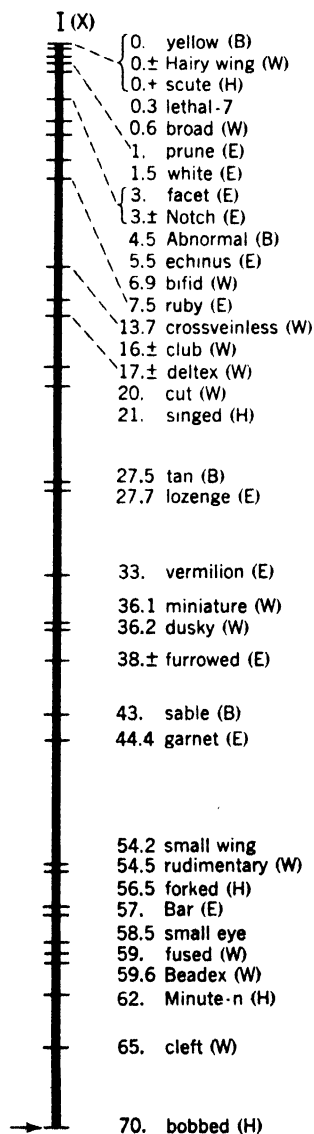




Fig. 494. Giant chromosomes found in the cells of the salivary glands of *Drosophila* larva.

enormous size makes possible detailed observations otherwise quite beyond the range of microscopic visibility. These chromosomes are identifiable by their patterns of transverse bands. By the study of deficiencies, these bands have been associated with the mutant genes known to be located in particular chromosomes. Thus by X-rays a chromosome may be broken into one or more pieces, and in the rearrangement and healing of the pieces a segment containing one or more bands may become lost altogether. The remaining chromosome will be shorter than before, and when a normal chromosome pairs with it in the salivary gland cells, the normal chromosome will buckle a bit at the site of the deficiency in its partner. If the normal chromosome carries a recessive gene, such as that for white eye color, in the region corresponding to that lost in the deficiency, the recessive gene will now lack any allele, and be able to manifest its effects in the eyes of the fly; that is, they will be white. Deficiencies have been found by breeders in many plants and animals besides fruit flies. For example, in mice a deficiency was discovered for a part

of the chromosome carrying the recessive gene responsible for the so-called "waltzing" of mice which are unable to walk straight but turn round and round in circles. Once, in a cross of a homozygous normal mouse with a homozygous waltzer, a cross which of course ordinarily produces only mice normal in phenotype, a single waltzing female was found. She was bred and her offspring, which should have carried a normal chromosome with the dominant alleles of the waltzing gene, were examined cytologically and found to have a chromosome with a large deficiency. It was this which had allowed the recessive gene for waltzing to manifest itself in the unexpected female.

Most deficiencies are, however, quite harmful to their carriers, and turn out to be lethal in homozygous conditions. They represent irreparable losses of hereditary material and consequently cannot be of major importance in evolution. The opposite sort of change, in which a chromosome arises with an extra group of genes, is generally not so harmful as a deficiency, and, indeed, furnishes about the only mechanism for the origin of new combina-

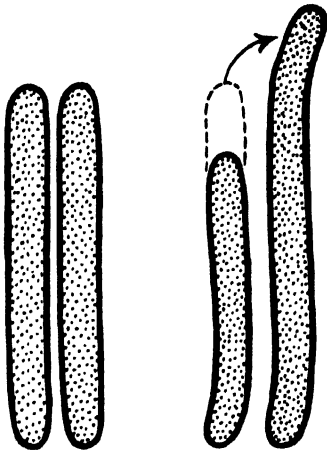


Fig. 495. Deficiency and duplication in chromosomes. A segment detached from one chromosome becomes attached to its partner.

tions, or even genes. This change, called a *duplication*, may arise together with a deficiency, if a piece is lost from one chromosome and transferred to its partner (Fig. 495). In breeding, the deficiency and duplication will be inherited by different offspring. The result may be seen in a mutant of *Drosophila* with narrow, strip-like eyes in place of the normal large oval ones. This mutant, a dominant, is called Bar. The giant salivary gland chromosomes of Bar-eyed flies can be seen to carry a duplication, or "repeat," of a segment

Fig. 496. Duplications involved in bar-eye and ultra-bar eye. Note that the region in "normal" indicated by bracket, is double in "bar" and triple in "bar-double."

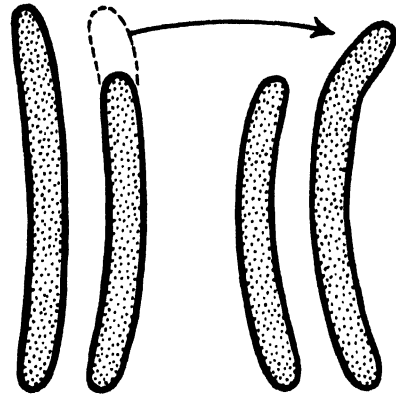
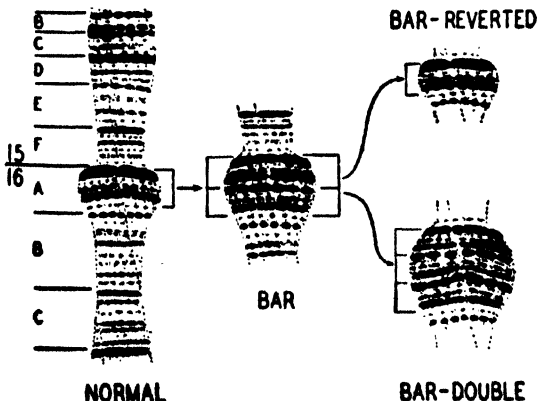


Fig. 497. Translocation in chromosomes by transfer of a segment to a member of another pair.

four or five bands in length and arranged in tandem with the segment normally present (Fig. 496). In an extreme allele of Bar with very tiny strip-like eyes, the segment, as the figure shows, was found to be triplicated. By further mutation of genes duplicated in such segments, perhaps altogether new kinds of genes might in time arise, since the extra genes would not be required for their original functions and might consequently mutate in ways previously not to be tolerated.

Translocations, in which segments are transferred from one chromosome to another, non-homologous to it, are of occasional importance in the evolution of species (Fig. 497). Most translocations, however, cause a considerable degree of sterility on account of the abnormal segregation of the chromosomes resulting at meiosis; and for this reason they do not play as important a role as the remaining major type of chromosome rearrangement, inversion, which has little or no harmful effect.

An *inversion* occurs when a single chromosome is broken in two or more places and a segment becomes turned end for end before being incorporated in the healed chromosome (Fig. 498). Inversions are very common in wild populations of plants and animals, and appear to be the principal natural agency

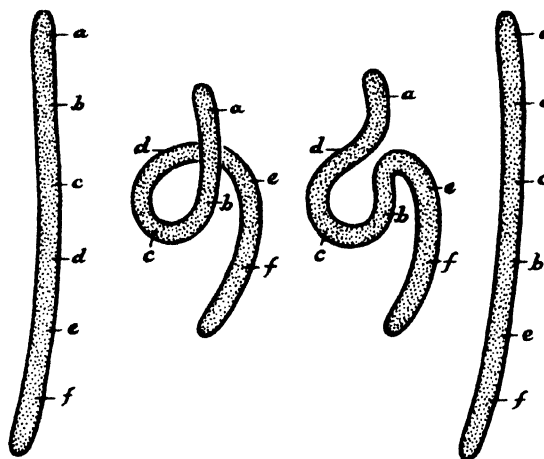


Fig. 498. Inversion of a segment of a chromosome. Note the change in sequence of genes between chromosomes at left and at right. Central figures indicate mechanism of inversion.

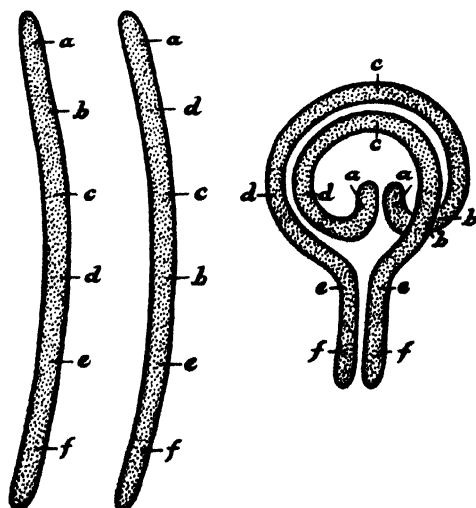
bringing about the rearrangement of genes in the evolution of races and species. This leads ultimately to such great differences that the chromosomes of the two forms, introduced into a hybrid, find it difficult or even impossible to pair with one another. In order to achieve synapsis at all, complex loop formations arise (Fig. 499). *Drosophila pseudoobscura* and *Drosophila miranda* are two species so similar that it is quite difficult to distinguish them, and each contains five pairs of chromosomes. They will mate and hybridize, but the salivary gland chromosomes show that repeated inversions have occurred, since the two species have diverged from their common ancestry. Now the chromosomes are unable to pair and segregate properly in a hybrid. In many species a similar situation leads to hybrid sterility, which perpetuates the genetic isolation of the two forms once they have diverged. In these two species of *Drosophila* the sterility of the hybrids is primarily due to many genes which have mutated to form two systems incompatible with one another. But two such systems could never arise without isolation of some sort to prevent random gene exchange between the populations — and the inversions appear to have played an important part in

establishing this isolation. Genes cannot be freely exchanged between two chromosomes, one of which carries an inversion and the other of which does not. Inversions interfere with normal crossing-over. As a result, each inversion that becomes by chance established in a population gradually acquires a unique group of genes selected for their fitness in the prevailing environment, and such inversions thus become a basis for the selection and differentiation of new species. Although it is not to be assumed that this process is responsible for the origin of every new species, it nevertheless seems to be quite common.

Position Effect

It has sometimes been found that a gene, when removed from its original position in the chromosome by one or another of the above types of rearrangement, manifests an alteration in its effects which is not due to a simple mutation. For example, it was found that the Bar duplication for eye shape in *Drosophila*, previously described, has a different effect when it is next to another Bar gene than when it is next to a normal non-Bar gene. Thus Ultra-Bar (triplicate Bar segments) heterozygous with normal (one Bar segment) produces a much smaller eye than homozygous Bar (two Bar segments in each chromosome). In each of

Fig. 499. Synapsis of an inverted with a normal chromosome. Peculiar twistings and loopings are necessary to bring alleles in opposition.



these genotypes the number of Bar segments is exactly the same, but the effect is different. Recessive genes may be made to become dominant by such shifts in position, and in some cases entirely new effects are produced. This position effect disappears when the gene, by a second rearrangement, is restored to its original spatial relations in the chromosome. The action of a gene can, then, be modified by its neighbors, and its customary action is in part due to its interaction with adjacent genes in its normal neighborhood. One might be tempted to think that maybe all "genes" are really just the interactions between adjacent parts of the chromosomes; but as a matter of fact only two species, *Drosophila melanogaster* and *Oenothera lundiniana*, an evening primrose, have ever manifested position effects, although in many other species, genetically well studied, position effects have been looked for. In maize, for example, chromosome rearrangements have been studied by the scores, but no position effect has ever been found. Moreover, even in *Drosophila* only a few particular genes manifest any kind of position effect, and the great majority of the genes exhibit exactly the same effect when in one position as when in another. There is consequently no real reason to question the differentiation of the chromosome into discrete units of specific effect, in other words, into genes, even though we must recognize that the effects *may* be modified by changes in the positions of the genes.

Polyploidy

Sometimes chromosome number in a zygote becomes increased because of a failure of meiosis to occur in a germ cell or maturing spore. Upon fertilization, this usually gives rise to forms with three complete sets of chromosomes instead of two. Such forms are called triploids. Doublings of chromosome number may also take place at any time in the life cycle by a duplication of chromosomes without a subsequent separation of them in the same mitotic cycle. This will give rise to tetraploid cells (with four sets of chromosomes), which may include in their later cell descendants

either somatic or germ cells, or both. It is interesting to know that malignant cancer cells are very frequently tetraploid or carry higher multiple sets of chromosomes. But before one jumps to conclusions, it is well to know also that virtually everyone has normal polyploid cells in his body, particularly in such organs as the liver. It has been discovered in recent years that there are a number of drugs of plant origin, such as colchicine, which readily induce the formation of polyploid cells.

The reproduction of polyploids is, from a chromosomal point of view, very disorderly. Triploids, in particular, find great difficulty in forming gametes with balanced sets of chromosomes, either haploid or diploid. Most of the time a gamete will get two representatives of certain chromosomes and only one of others. This is very much more detrimental in effect than a simple increase from diploid to triploid or tetraploid, which does not modify the relative numbers of the genes in different chromosomes but maintains the same "chromosome balance." As a result, triploids produce very few healthy offspring and are as a rule highly sterile. Tetraploids, however, because they have four chromosomes of each sort, can assort them at meiosis by two's, and so produce diploid gametes that will have a normal chromosome balance. Tetraploids consequently show only a moderately reduced fertility, and often, being characteristically rather larger and more vigorous than diploid individuals, are better adapted than the latter. Thus, in spite of lower fertility, they rather often become established in nature as races, which may eventually be transformed by mutation and isolation into full species. The results of this are to be seen in many groups of plants, in which related species have chromosome numbers that form a series of multiples. Different species of meadow-rue, an old European medicinal herb, for example, have the chromosome numbers (haploid): 7, 14, 21, 28, 35, and 42. There are three groups of species of wheats, with the haploid chromosome numbers 7, 14, and 21, the cultivated wheats falling into the two latter, and especially into the last, of these

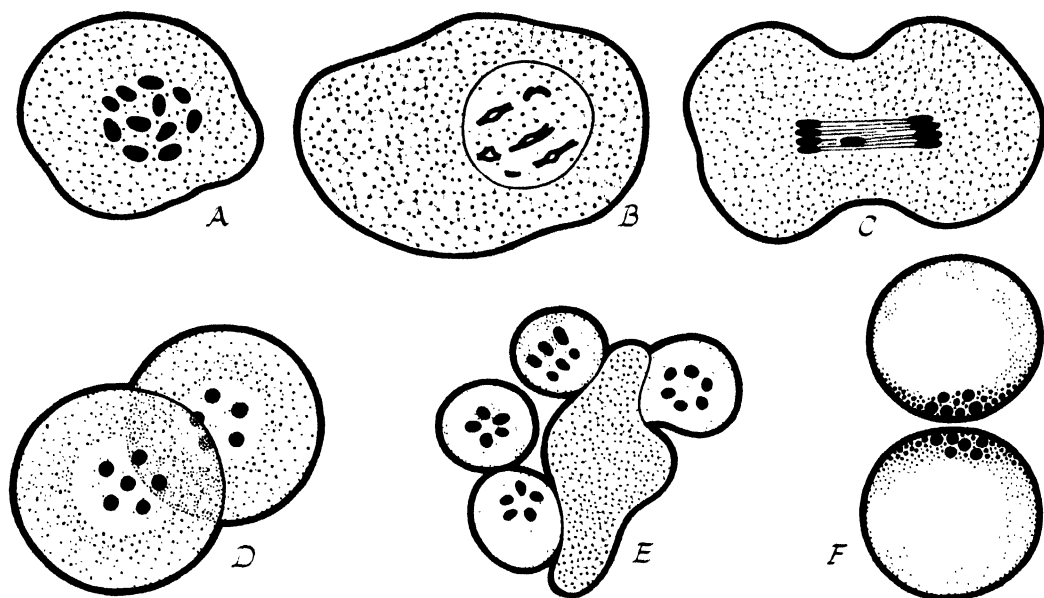


Fig. 500. Stages in spermatogenesis of the Nematode *Ancyracanthus cystidicola*. A, spermatogonium showing 11 chromosomes; B, synapsis and tetrads; note one lone chromosome; C, first meiotic division; note unpaired chromosome (X) passing to cell at right; D, two secondary spermatocytes after reduction division, one with five, the other with six chromosomes; E, the four spermatids; F, the two types of spermatozoa produced. (After K. Muslow)

groups. Polyploidy is of great importance to plant breeders.

The Sex Chromosomes

Speculation as to the manner in which sex is determined has been rife for ages, and many people living in civilized communities today still cling to ancient beliefs about it. It was thought that all sorts of environmental factors act in determining sex, even as they were thought to determine other inborn factors. Expectant mothers engaged in beautiful but futile immersion in music, art, and "the finer things of life," in an earnest attempt to inculcate an appreciation for such things into their unborn; and similar futile methods were employed in an effort to influence the sex of the baby to be.

In 1902 the American zoologist McClung found visual evidence of sex-determining mechanism in the chromosomes of the grasshopper, and others soon showed how it worked. Whereas chromosomes in diploid cells are normally paired, one chromosome (called the X chromosome) in the male cells lacks a partner. In females, however, the X chromosome has a regular partner like itself; that is, there are

two X's. Hence the male cells produce in meiosis two varieties of sperm cells in equal proportions, while all egg cells are alike. The sperm cells carrying a full complement of chromosomes produce zygotes with an even chromosome number which grow into females, while those lacking one chromosome determine the male. Sex is thus determined by the heterozygous XO condition of the male, resulting in sperms either carrying or lacking the X chromosome (Fig. 500).

With certain variations, this sex-determining principle operates in most higher organisms, including mankind (Fig. 501). Where in some insects (grasshopper) the female is represented by XX and the male by XO, in others, as in *Drosophila*, the female is XX, while the male, instead of lacking a partner for his X, has a differently shaped chromosome, called the Y chromosome, which acts as a partner to the X, thus giving XY. In this situation, all eggs are as before genetically alike with respect to sex, and any one of them may give rise either to male or female offspring, depending only upon whether an X-bearing sperm or a Y-bearing sperm fertilizes it. It is clear, though, that the

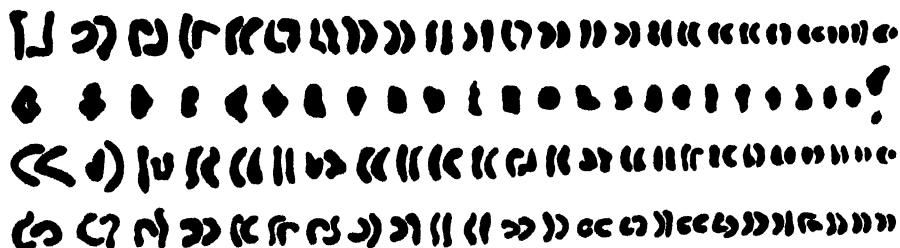
sex is determined at the very moment of fertilization. In other animals, as in birds, butterflies, and some fishes, the condition is reversed — all sperm cells are alike, while there are two kinds of eggs with respect to sex chromosomes. But the end result is the same — a fifty-fifty sex ratio determined from the instant of fertilization.

The determination of sex is not, however, answered by these observations. Is it the single X in a male or is it the Y chromosome which is the determiner of maleness? Is femaleness the result of a double dose of X ? Abnormal chromosome conditions provide the answer. By non-disjunction, fruit flies may be obtained which carry two X chromosomes and a Y as well. These XXY individuals are normal, fertile females. Also flies with only one X and no Y can be obtained. These, although sterile, are perfectly formed males. This is simple proof that the X , and not the Y , is instrumental in determining sex. But sex in all organisms is a relative matter. Thus, in mammals, including man, the organism starts out a sexual neuter, anatomically neither male nor female, but with potentialities for both. In some organisms, sex is determined entirely by a simple response to environmental conditions. Thus in the worm *Bonellia*, larvae settling upon the proboscis of a female become dwarf males, and those settling down in any other situation become females. Numerous similar cases are known. In many animals, under intermediate conditions, intermediate sexes or intersexes may develop. In higher organisms, however, as in man, sex is determined at the moment of fertilization.

But even in these higher species, where the chromosome constitution has become the dominating factor in determining sex, the secondary sexual characteristics are hormone-determined, and a deficiency of these hormones, as following castration, causes changes in the sexual characteristics of the individual. The genes responsible for the sex characteristics of the organism produce their result through the medium of hormones, and if their means of expression is removed, the characteristic is altered despite the continued presence of the sex-determining genes. This, however, is no more remarkable than that the genes affecting hair color no longer express themselves in a bald person. Hormonal influences may even change the primary sexual structure of an organism. In cattle when twin embryos of opposite sex have common circulation by fusion of their blood vessels, the female calf is rendered sterile, remaining a sexually undeveloped "freemartin," due to her early exposure to the male hormones of her twin brother. In birds and mammals, sex may even be temporarily reversed by large doses of hormones of the opposite sex given early in life. So we are led to the conclusion that every individual carries all the necessary genes for the realization of either male or female sex characteristics, and one chromosome pair, the sex chromosomes, tips the balance one way or the other. But probably no single gene can be identified as *the* sex gene, for in *Drosophila* every portion of the X chromosome has been proved to possess sex determining powers.

That the other chromosomes (autosomes) also have something to do with sex determina-

Fig. 501. The 24 pairs of human chromosomes, arranged in order of size. Three top rows, male. Top row, cell from germ line. Second row, meiotic cell with homologous chromosomes in synopsis. Third row, from a somatic cell. In all three lines of male cells, the X and Y chromosomes are shown at the extreme right, the Y chromosome being the smallest. Bottom row, chromosomes from female somatic cell. Note that here all chromosomes are evenly paired. (From Painter, after Evans and Swezy)



tion is shown by the aberrant individuals produced in *Drosophila* by various forms of non-disjunction in the offspring of triploid females. Besides the normal diploid XY males and XX females the following genotypes are known: (The symbol A stands for one complete set of autosomes):

			Ratio of X : A
XXX	AA	superfemale	1.5 : 1
XXX	AAA	triploid female	1 : 1
XX	AA	diploid female	
		(normal condition)	1 : 1
XXY	AAA	intersex	1 : 1.5
XY	AA	diploid male	
		(normal condition)	1 : 2

This indicates that normal sex balance, either male or female, is obtained by a specific ratio between X-chromosomes and autosomes. A ratio of 1 : 1, whether diploid or triploid, releases female characteristics; a ratio of 1 : 2 male. Where the ratio is abnormal, as 1 : 1.5, an intersex develops, or conversely (1.5 : 1), a superfemale with exaggerated female characteristics, but sterile.

The Sex Ratio

We have seen that the mechanism of sex determination automatically produces a sex ratio of equality between males and females. But again in many species, observed facts are at variance with our expectations. Despite the fact that in man, for example, the prenatal mortality of males greatly exceeds that of females, there are still approximately 105 males born to every 100 females born. Since the production of X- and Y-bearing sperms in equal numbers is indisputable, this can only mean that Y-bearing sperm cells are on the whole successful in reaching the egg cell ahead of the X-bearing sperms. Why this should be so no one can say, for there is no discernable difference between them. It has been established statistically, though, that sperm cells are really of two sizes, for measurements of sperm cells fall into a bimodal curve, and it is not difficult to guess that those bearing the Y-chromosome are slightly lighter and smaller. Whether it is

this infinitesimal difference in mass, or whether the difference lies elsewhere, some such difference must be postulated. It is the dream of many a practical-minded investigator to find some simple method by which the sperms with X's may be segregated from sperms with Y's, for this would make it possible to pre-determine sex. Its value in animal husbandry would be considerable, but thus far, all attempts have failed.

Sex Linkage

Besides carrying the gene or genes that tip the balance in sex determination, the X-chromosomes are known to have on them many other genes in no way associated with the function of sex. Since X-borne genes are on the same chromosome with the sex-determining genes, they are linked with these, and are thus said to be sex-linked. Such genes are inherited in a peculiar manner because of the sex difference in distribution of the X- and Y-chromosomes, and because many of the genes on the X- have no alleles on the Y-chromosome, and some of the few genes on the Y-chromosome have no alleles on the X.

We may first consider the effects of one of those few genes which lie on a segment of the Y-chromosome not homologous to any part of the X-chromosome. Perhaps the most conspicuous is a form of *ichthyosis* (fish-skin disease). In this affliction the skin becomes bark-like and almost black, reaching a thickness of $\frac{3}{4}$ inch, while only the face, the palms of the hands, and the soles of the feet remain normal. The condition was first noted in the son of an English country laborer and came to the attention of the Royal Society in 1731 and has been traced through five subsequent generations, the first afflicted male having six sons, all of them with ichthyosis. In subsequent generations — some found wives! — all sons inherited the peculiar skin from their fathers, but no daughters ever had it or ever transmitted it to any of their descendants. Only a Y-borne gene could behave so, for its inheritance strictly follows the Y-chromosome. All sons receive it from their fathers, and daughters never do.

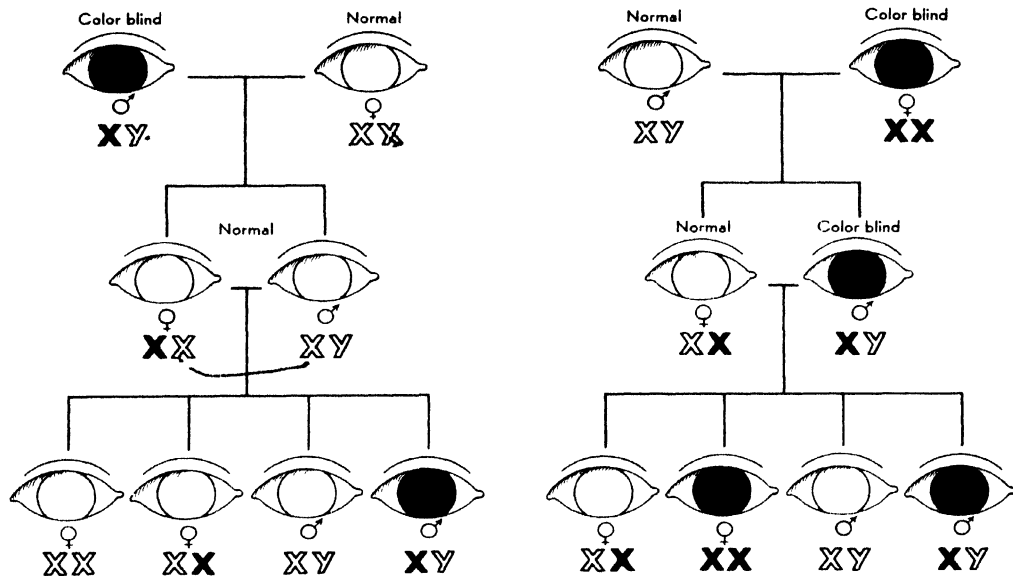


Fig. 502. Inheritance of red-green color-blindness. Gene causing color blindness is indicated by solid black X. Color blindness indicated by black eye.

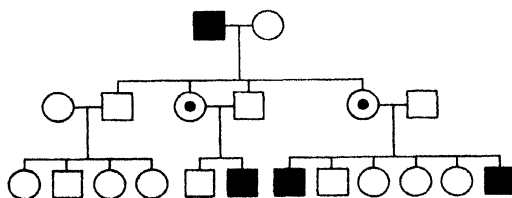
X-borne genes with alleles on the Y-chromosome behave much like ordinary autosomal genes, so we pass on to consider here the mode of inheritance of those genes borne on the non-homologous section of the X-chromosome, and hence without Y-borne alleles. Such genes, whether dominant or recessive, always manifest their effects in those males who inherit them and who, having only the one X-chromosome, cannot also inherit a normal allele. Since the abnormal genes are rare, females who carry an X-borne recessive gene are usually heterozygous, and the dominant normal allele prevents its expression. This produces the pattern of inheritance illustrated by common red-green color-blindness (Figs. 502 and 503).

Here (Fig. 502) a color-blind male with a normal wife produces children all of whom appear to be normal. Since all daughters must have received an X-chromosome from each parent in order to be daughters, they must all have received the gene for color-blindness from their color-blind father, for this is the only kind of X-chromosome he has. But no son ever inherits an X-chromosome from his father, for he has only one, and that he gets from his mother. Hence the father cannot transmit color-blindness to his sons, nor can these, lack-

ing it, transmit it to their descendants. Although all of his daughters carry the gene for color-blindness, and are thus carriers, they will be phenotypically normal, for the dominant allele for normal vision, inherited from the mother, will be decisive.

A carrier daughter, with a normal husband, transmits the defective X-chromosome to one half of her children, either sons or daughters. Thus half of her sons receive the defective gene, and having no normal allele, are color-blind. Half of the daughters, too, inherit the defective gene, but the normal X-chromosome of the father suppresses its expression. Thus the sex-linked trait is handed down from grandfather to grandson via the unaffected mother. This is the normal pattern of sex-linked X-borne inheritance, and applies to other factors in man such as the bleeding sickness (hemophilia),

Fig. 503. A family history of red-green color-blindness. Square signifies male; circle, female. Solid black indicates color-blindness. Dot in circle indicates normal carrier.



optic atrophy, and others. The pattern of inheritance when both parents carry the factor is also shown in Figure 502.

Sex-influenced Characteristics

Certain traits determined by autosomal genes may behave in a manner often confused with sex-linkage. Baldness is probably among these. Genes predisposing to baldness act more strongly under male metabolic and hormonal conditions so that baldness is dominant in men but recessive in women. The claim that eunuchs do not become bald lends weight to the interpretation. A similar pattern is known in cattle. An autosomal gene causes a color pattern of mahogany and white in cattle homozygous for it (MM). The recessive (mm) is red and white. Heterozygous individuals (Mm) are mahogany and white in males, but red and white in females. Thus the expression of M versus m is clearly so delicately balanced that the metabolic difference between male and female is enough to permit either the one or the other to express itself. The development of horns in certain breeds of sheep follows a similar rule.

Conclusion

When we survey the history of genetics, we are struck by a combination of contradictory facts. Knowledge of the existence of heredity probably dawned with the first glimmering of human intelligence. Realization of the truth that like generally begets like led men to make

slow but marked improvements in domesticated plant and animal stock by selection. It is consequently somewhat startling to learn that a real understanding of hereditary processes is hardly fifty years old, and that only since 1900 was the doctrine that "like begets like," as applied to the individual case, clearly recognized as fallacious. Striking, too, is the basic simplicity of the mechanism that serves as a bridge connecting the present generation with those of the past. But at the same time we cannot help a degree of amazement at the inexhaustible variety which arises out of the basically simple plan. Again, even as we marvel at the ultimate living qualities of the genes, which reproduce themselves so perfectly and guide the intricate course of development so unerringly, we must recognize too their basic dependence on their environment, both external and internal. We are led to appreciate the fundamental interdependence of heredity and environment, and realize the futility of trying to decide which of the two is the more important, for each is the instrument of the other. We understand now the power of a knowledge of genetics in the shaping of the organisms of tomorrow, and we recognize too its limitations. Man has taken a decisive first step in the enduring effort to improve the organisms upon which he depends, but the compelling realization that he, the master, is also the subject, is but slowly dawning upon his collective intelligence. This will be the subject of our final chapter.

Human Genetics and Eugenics

Out of the welter of organic evolution there has finally emerged one creature which may in the future control, shape, or exterminate any other form of life. For this compelling biological reason alone, *Homo sapiens* deserves highly special consideration. That this also coincides with our natural interest and curiosity about our own species is merely incidental. Man's dominance stems not only from his accumulated understanding and consequent improved control, but from a rising tide of numbers. After 500 centuries of human evolution the earth's population, by the middle of the nineteenth century, reached the 850 million mark. Now, only one century later, this number has doubled, and at the present rate of reproduction it will double again in the next. Great changes in the balance of nature are therefore inevitable.

The Problem of the Future

Man, like other creatures, is the product of the selective action of natural forces on his plastic germ plasm. There is no reason to assume that this plasticity has become any less than it ever was, and since at every turn man has tampered with the selective forces that in the past have shaped him, new changes are to be expected. Some few organisms have existed for hundreds of millions of years almost unmodified. *Lingula*, buried in the sands of the ocean bottom, lives in a segment of earth that has hardly changed since the oceans were formed. How different the environment of man! If he is to survive, change for him is inevitable. Before the advent of civilization, and especially of science, only those escaped death by violence, starvation, and disease, who had the genetic constitution for strength, cunning, and foresight — and a suitable physiological constitu-

tion. Their descendants survived in turn if they inherited the necessary genetic constitution. Thus human germ plasm was constantly pruned by the environmental demands.

But man has changed his environmental scene. Inroads of war, floods and automotive massacres notwithstanding, law and order supported by science and medicine have reduced death by violence and disease in cultured countries, and survival no longer necessarily goes to the strong. Today, each month adds to the total world population enough people to populate a Boston, a San Francisco, or a Philadelphia. This of course cannot continue indefinitely, but while it does, the new patterns of living and of social relationships, simply by changing the pattern of selective action, will leave their mark on the human germ plasm.

Science has been partially successful in analyzing some of the past interrelationships that produced modern man, and by applying these to present and to possible future conditions, we can predict — not where man is going — but where he *may* go, under the influence of certain existing or assumed future selective factors. It is the duty no less than the privilege of modern civilized free man to scrutinize the possible paths that extend into tomorrow, so that he may contribute his mite toward shifting evolution in whatever direction appears to him most desirable. Before he can do this he must decide how he would have mankind changed, had he the power. He must have a reasonable understanding of the potentialities as well as the limitations presumably inherent in human germ plasm. He must above all arrive at the full realization that man, the evermore powerful master, is at the same time the subject of his own newly acquired creative powers.

It is with these weighty problems and profound responsibilities in mind that we undertake to survey some of the highlights of what is known about human genetics, about the effects of improved environmental conditions on man (euthenics), and about the possibilities of improving our species by careful selection of parental stock (eugenics).

How People Vary

People vary in all sorts of ways, in stature, color, proportions, resistance to disease, temperament, and intelligence. Knowing what we do about genetics and evolution, we welcome a certain degree of variability, for we know that the lack of it spells stagnation and eventual extinction. But some individuals are unquestionably inferior to others in certain respects — physically, temperamentally, and intellectually. No one is likely to argue in favor of the sort of variation that produces imbeciles and idiots — or blind, deaf, or limbless human beings. Great virtues though some persons of the latter classes may possess, they (and we too) would be better off if, in addition to their virtues, they had all other normal faculties. And there is no dearth of human germ plasm. However, no one today is astute enough to decide categorically what human variations are best or most desirable, especially for unknown future conditions. But normal individuals will probably concur that the human race should be preserved, and that it should become "better."

But what is "better"? Standards vary from race to race. Dusky races do not consider light skin either lovely or desirable. Some look upon blue eyes with abhorrence, while others write poems about them. Most people feel, justifiably or not, that with the possible exception of the "genius," a marked deviation from the norm is undesirable. They will probably agree, however, that an improved mean standard of intelligence, of physical perfection, and of health would be beneficial.

Genetics and evolution shed light on how man has come by his present standards, imperfect though they are. We know now that in the past unfavorable variations simply failed

to survive. Today, the hazards of civilization are still great. Many children become defective because of preventable disease or malnutrition. Detrimental environmental conditions, often in the home itself, cripple thousands mentally and spiritually. Our knowledge of genetics reassures us that such defects are not transmitted to the next generation, at least not via the germ plasm. But handicapped parents, especially those mentally crippled, are often incapable of providing the best environment for their children, and thus a new generation starts at a disadvantage. What is far more serious — tens of thousands of human beings are born defective, and of these defects, many are hereditary. No longer, as in a state of nature, are such stunted or defective individuals eliminated, nor would the ethics of human civilization condone their elimination. The capable accept the burden of care, but the intelligent do not accept it unquestioningly. Is it necessary that so many human beings should be physically or mentally crippled? Is it possible to reduce the number of misfits by improving environmental conditions, that is, by measures of euthenics, or by the careful selection of parent stock, that is, by eugenics? To answer these questions it is necessary to establish by observation and by experiment the relative roles of environment and heredity, remembering that these are inseparable members of a team.

HUMAN GENETICS

As an introduction to a survey of human genetics, a table of some of the normal and abnormal characteristics of which the nature of inheritance is known is given on the opposite page. Symbols indicate the nature of the gene as to dominance, recessiveness, or other type.

Problems and Facts

To ask which is the more powerful factor in shaping an individual — nature or nurture, heredity or environment? — is like asking which is more important, the bow or the arrow. Instead of trying to answer such a question, it is far better to determine the role of each in

producing a desired effect. Except for identical twins, all human beings differ from each other by heredity. No amount of environmental influence can transform a white into a Negro or vice versa, yet exposure to sunlight may darken a white man or confinement in the dark may lighten a Negro. Theoretically, it should be possible to improve a race by selecting as parents for future generations only those individuals known to carry desirable genes. But the problem is far from simple.

A dominant gene may be eliminated from a

race in a single generation, if each individual bearing the gene clearly advertises the fact. But a simple recessive can never be completely eliminated from the human germ plasm, even if we discount new mutations. A common recessive may be reduced from, say, 25 per cent to 11.1 per cent in a single generation. But as it becomes rare, its further reduction becomes increasingly difficult, so that even by eliminating all those individuals who show it (the homozygotes), a reduction from 0.1 per cent to 0.06 per cent would require 300 years!

SOME HEREDITARY HUMAN TRAITS

GENERAL STRUCTURAL

0 albinism (no pigmentation; some forms dominant)

- piebald (spotted pigmentation)
- freckles
- dark hair
- red hair
- hypertrichosis ("dog-faced" man)
- (♂) baldness
- * ● brown eyes
- * ♂ color blindness
- * ● congenital cataract
- high myopia (excessive corneal curvature)
- high myopia (long eyeball)
- astigmatism (irregular corneal curvature)
- * ♂ (Y) ichthyosis hystrix gravior (thick skin)
- " " stature
- brachdactyly (short digits)
- * ● achondroplasia (short limbs)
- "lobsterclaw" (split hand or foot)
- " " head shape
- deaf-mutism

SYMBOLS

- recessive
- dominant
- ♂ sex-linked
- (♂) sex-influenced
- " " multiple factors
- * traits treated in text
- (Y) borne on the Y chromosome

CHEMICAL

- * ● blood groups A₁A₂A₃B (5 or more alleles)
- * ○ blood group O
- * ● Rh factor (6 or more alleles)
- * ♂ hemophilia (bleeders)
- diabetes mellitus
- allergies (tendency)
- ? susceptibility to tuberculosis
- * ○ phenylpyruvic amentia (lack of an enzyme, causing idiocy and light hair)

NERVOUS

- " " intelligence
- mental deficiency (some forms)
- * ● Huntington's chorea (a form of St. Vitus' dance)
- amaurotic idiocy (degeneration of central nervous system)
- * ○ microcephaly (small-headed idiots)
- deafness (auditory nerve atrophy)
- tasters (phenyl-thio-carbamide)

By their very abundance, common recessives like blue eyes, or blood type O, indicate their harmless nature and hardly call for elimination. It is the rare recessive, like certain forms of mental deficiency or some forms of albinism, that are harmful and could well be eliminated. Since their elimination is all but impossible, it has been argued that any program of negative eugenics, by segregation and sterilization, would be futile, and hence that we had better do nothing about the matter at all. This is like the lazy man's argument that since he can never eradicate the last weed out of his garden — and even if he did, new ones would appear anyway — he might as well do no weeding at all! The aim of negative eugenics would then appear to be not the creation of a race free from harmful genes (an impossibility), but rather the prevention of their gradual increase with a subsequent deterioration of the race. There is hardly a human being that does not carry some decidedly harmful or even lethal gene. Only elimination of the entire human race would eradicate them. But their undue increase can be, and evidently must be, controlled. Similarly, efforts to increase the percentage of favorable genes by positive eugenics, that is by increasing the reproductive rate of those known to bear them, could raise the general quality of the race. Under all circumstances, improved environmental conditions, or measures of eugenics, should be provided to give the favorable gene combinations every opportunity to realize their potentialities.

From a study of the transmission of human hereditary characteristics it is evident that heredity in human beings is basically no differ-

ent from that in other organisms. Observed factors range over the whole field of structure and behavior. A few of them will serve to illustrate the Mendelian nature of their inheritance.¹

Some Hereditary Factors

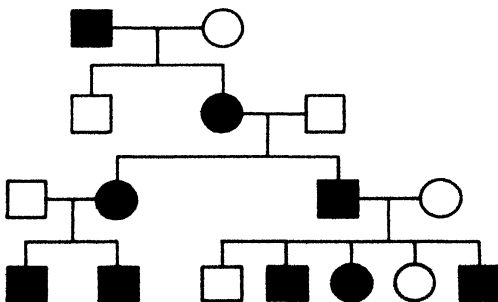
Congenital Cataract. Cataract is an opacity of the lens of the eye, and produces various degrees of blindness. Although it may be induced by external agents such as heat, light, or contusion, some forms are heritable, and studies of family pedigrees show that it appears to be caused by a simple dominant gene (Fig. 504). The pedigree shows that the characteristic is inherited irrespective of sex, that only one parent of an afflicted child generally has it, and that an afflicted parent does not transmit it to all his children, but by and large, only to one-half of them. Hence the afflicted parent must be heterozygous and the gene is dominant.

Eye Color. Eye color is determined by the joint action of at least 5 pairs of genes. First there must be present a dominant gene for pigmentation. Its absence causes albinism. A second dominant gene causes two layers of pigment to be deposited — one brown layer on the anterior of the iris surface, and one posterior refracting pigment layer. The recessive allele of this gene causes absence of the anterior brown layer and the refracted light from the posterior layer then produces blue or gray eyes. Two or more gene pairs determine the shade of the anterior brown, while others influence its distribution (speckled or streaked). Since the dominant gene for anterior brown usually produces the most striking effect, we may, for practical purposes, consider brown eyes dominant and blue or gray recessive.

Achondroplasia. This abnormal characteristic presents several features of unusual interest. It presents itself primarily as an extreme shortening of the long bones, producing a very characteristic type of dwarf (Fig. 506). Study of the mode of inheritance of this disease is difficult because many afflicted individuals do not have progeny. The pedigree given shows

¹ Ichthyosis, baldness, color blindness, and hemophilia were discussed in Chapter 24.

Fig. 504. A pedigree of congenital cataract. Squares indicate males, circles, females. Solid symbols indicate defective individuals.



why the gene is thought to arise spontaneously by mutation, then to be handed on as a simple dominant, skipping no generation (Fig. 505).

Hemophilia. This sex-linked recessive characteristic, located on the X-chromosome (pages 572-575), causes failure of the blood to coagulate normally, resulting in grave danger to life. Under primitive conditions, hemophiliacs would not survive many years. With modern medical care and protection, they may do so, and thus can perpetuate the gene. The pedigree of the descendants of Queen Victoria of England clearly shows the manner of transmission (Fig. 507).

Blood Groups. In recent years numerous chemical differences in blood have been found, and these are known to be specific individual characteristics, like eye color, hair color, or any other heritable characteristic. Research has uncovered unexpected complications and ramifications. There are many different series or sets of blood groups in man; the three best known are the ABO blood groups, the MN series, and the Rhesus (Rh) blood groups. In all cases, the red blood cells carry specific antigens which, when transfused into a person of a type not carrying such an antigen, cause the formation of specific antibodies. If the transfusion of the same type is ever repeated, the antibodies will now be able to react with the complementary sort of antigen in the introduced red cells, causing them to clump or agglutinate, or even to dissolve. Either result is dangerous or even fatal. In all these series, the blood types appear to be under the control of

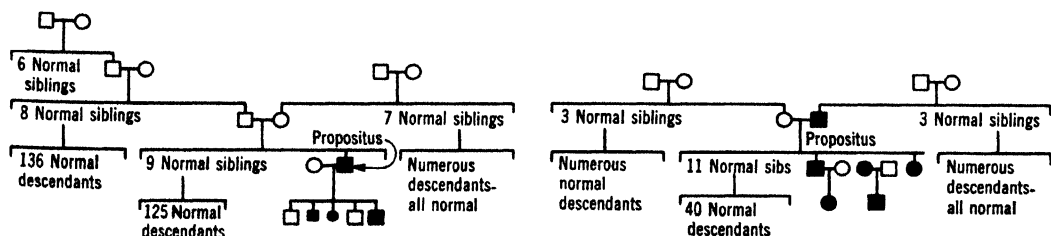


Fig. 506. Two generations of achondroplasia. Father's height 41.2 inches. The body and head are of normal size, the root of the nose is sunken. The characteristic appears to be inherited as a simple dominant, but appears rather frequently as a mutation in Scandinavian populations. Could they be the source of legends about gnomes?

multiple alleles, from three to eight or more in number, or perhaps of several closely linked gene loci. No decision is yet possible between these theories.

A brief look at the Rh factor relationships will serve for the whole group. Discovered in

Fig. 505. Two pedigrees of achondroplasia. The abnormality may arise suddenly in families previously showing no trace of it. Upon its incidence, it is regularly transmitted to about 50 per cent of the offspring as would a simple dominant.



1940, this antigen, first found in the red blood cells of Rhesus monkeys, induces formation of agglutinins (antibodies) in individuals who do not carry it. About 85 per cent of human beings have the Rh antigen and are said to be Rh positive. The blood of the other 15 per cent contains no Rh antigen — they are Rh negative. Certain fatalities in blood transfusions and certain forms of anemia and still-births have been traced to this factor. The gene responsible for the Rh antigens always produces them when it is present. If an Rh negative woman marries an Rh positive man, her child may be Rh positive. In about 5 per cent of cases, placental breaks allow some of the fetal red blood cells to pass into the bloodstream of the mother. She then manufactures Rh antibodies and these, passing into the placental circulation of the fetus, cause it to develop a blood disease called erythroblastosis. The child is then born either highly anemic and jaundiced or dead. The first child is almost always born before the immunity reaction of the mother becomes established, and so may escape any such ill effect, but subsequent pregnancies may be entirely unsuccessful unless special transfusion techniques are applied. If the mother has had a previous blood transfusion of Rh positive blood, even the first pregnancy may be unsuccessful.

The complexity of heredity is well illustrated by subsequent developments in the analysis of

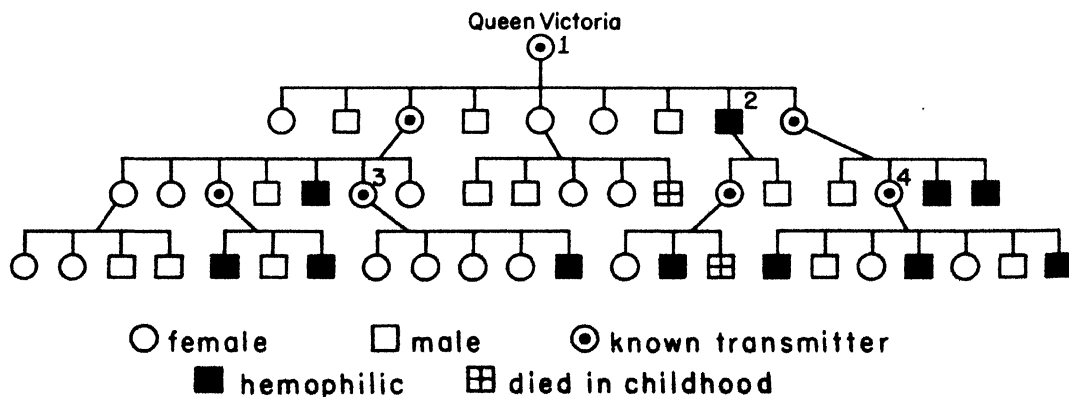
this series, for no less than eight major different Rh phenotypes, and many minor ones, have been established. The eight major Rh types may be due to a series of eight alleles (rh, Rh'', Rh', Rh⁰, Rh², Rh³, Rh¹, and Rh⁴, each producing a different phenotype. Or, alternatively, the interaction of three pairs of closely linked alleles, Cc, Dd, and Ee, would also produce eight different phenotypes (CDE, CDe, CdE, Cde, cDE, cDe, cdE, and cde). The Rh factor well illustrates the detailed and complex manner in which genes govern even the most minute chemical peculiarities of organisms.

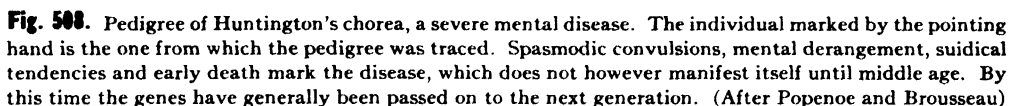
Since such blood types are heritable, and, except for the Rh types, appear to have little or no direct selective value, the study of the geographical distribution of such genes in the various races and subraces of the world has been intensively pursued, in the hope that it may establish relationships or yield clues to relationships otherwise obscure. Many racial patterns of blood types have actually been established. It is clear, too, that in some cases such typing can establish or, more readily, disprove parentage. For example, two Rh negative parents could not well produce an Rh positive child, except by an unlikely mutation.

Heredity in Nervous Structure and Function

No group of characteristics is of greater importance in man than those concerned directly

Fig. 507. Hemophilia in the descendants of Queen Victoria of England. The characteristic is sex-linked, transmitted through the female to the male, where it becomes apparent. 1. Queen Victoria of England. 2. Leopold, a hemophilic. 3. Alexandra, wife of Tsar Nicholas II of Russia, a carrier. 4. Victoria Eugenia, wife of Alfonso XIII of Spain, a carrier, mother of Alfonso of Spain, a hemophilic. The spread of the affliction from the single carrier mother Victoria is impressive, for 11 hemophilics are shown in the three succeeding generations.





Huntington's Chorea. A tragic degenerative disease of brain structure, this condition frequently does not become apparent until middle age. Choreics suffer from uncontrolled muscular movements, jerkings and twitchings of limbs and facial muscles. The disease frequently leads to mental derangement and to antisocial and suicidal tendencies. Most cases resident in the United States trace back to

three men, probably brothers, who, with their wives, arrived here from England in 1630. Of several thousand descendants of these men, about half of the children of affected persons have developed the disease in each generation. Many who did not developed other nervous disabilities, including epilepsy, infantile convulsions, or feeble-mindedness, not to mention inevitable anxiety complexes. Many members of these families are of average or better intelligence and live in full awareness of their threatening heritage, which may not show itself until between the ages of 25 and 55 (Fig. 508). The worst aspect of this terrible heritage is that no child of an affected person can know whether or not he too is a bearer who will pass it on to half of his children, until he has reached middle age and has already produced all or most of his offspring.

Microcephalic Idiocy. A simple recessive gene is probably responsible for the condition shown in Fig. 509. Its mode of transmission is indicated in the pedigree shown in Fig. 510. Afflicted individuals would then have to have two genes for the characteristic. Heterozygous individuals would be normal in phenotype. What value would you place upon the sibs (*i.e.*, brothers or sisters) of a microcephalic idiot as parents?

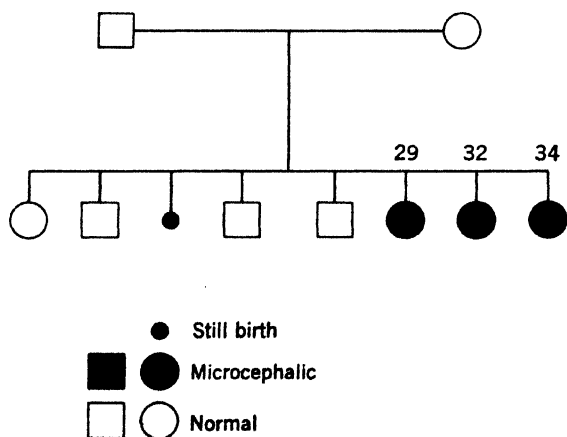
Phenylpyruvic Amentia. Genes are generally considered to produce their effects by controlling or modifying chemical processes within the

cell. In this connection a form of idiocy called phenylpyruvic amentia is of particular interest. Here a metabolic deficiency, evidently a loss of the ability to produce a specific enzyme for the oxidation of the amino acid phenylalanine, causes the afflicted person to excrete phenylpyruvic acid in the urine. This relationship between a metabolic defect and a mental defect is perhaps unusual only in the sense that no other examples have been discovered at the present time. Here the relationship has been recognized. The mode of inheritance is indicated in Fig. 511.

Schizophrenia (*Dementia Praecox*). This term embraces a complex of mental diseases ranging from "queerness" to complete apathy or to the delusions of grandeur or persecution. This type of mental disease constituted 18 per cent of the almost half a million patients in mental hospitals in the United States before World War II. New York state hospitals report a total of 37,000 schizophrenics, and since such cases are largely permanent residents, the expenses involved are heavy. Studies of relatives of schizophrenics clearly show the hereditary nature of the disease. Studies by Kallmann show that 68.1 per cent of the children of two schizophrenics themselves become afflicted. Among twins, the coincidence of schizophrenia in monozygotic twins is 68 per cent, but among dizygotic twins of the same sex only 15 per cent. Still, what is inherited is clearly not the insanity itself, but a particular genotype marked by a high vulnerability, or lack of capacity to remain normal under stress. Probably determined by one or more recessive genes, schizophrenics are usually produced by parents of normal phenotype. For this reason, neither segregation nor sterilization can eliminate the genes involved. The impracticability of applying any such measures to all the relatives of schizophrenics, normal or not, is obvious, in view of their numbers.

Deafness and Blindness. Of the 120,000 afflicted with loss of hearing in the United States, 10 to 25 per cent are considered to have an hereditary type, and of the 200,000 blind, as many as 25 per cent have an hereditary type.

Fig. 510. A pedigree of microcephaly.



Figures 29, 32 and 34 indicate age of the mother at the time of pregnancies

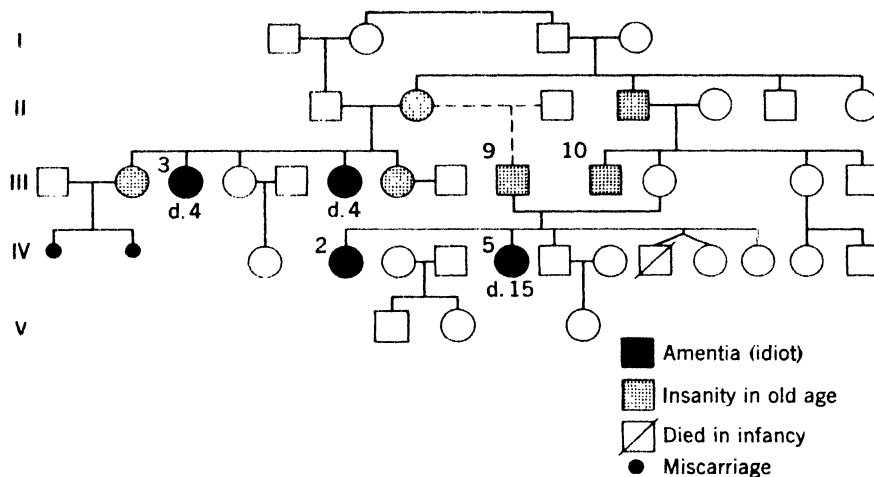


Fig. 511. A pedigree of phenylpyruvic amentia, a mental defect due to hormone deficiency. The characteristic behaves as a simple dominant, evidently modified by other factors. (After Penrose)

INTELLIGENCE AND HEREDITY

Is Intelligence Inherited?

No other question of human genetics is of greater potential importance than this one, and few are more difficult to answer. We know today that intelligence is complex. It is no single factor, but rather a complex of many talents or aptitudes, notwithstanding the fact that a single mutant gene may in some cases banish every trace of it. If simple eye color is controlled by no less than five pairs of genes, it is little wonder that intelligence should be far more formidable to analyze.

What Intelligence Is. The composite nature of intelligence becomes apparent in numerous ways. A normal, intelligent man, for example, may have greater difficulty in solving a given three-dimensional puzzle than some institutionalized idiots. Or again, some idiots may possess a greater mathematical aptitude or more musical ability than many a normal person. Individuals inept as students have sometimes achieved brilliant careers as businessmen, or even inventors or research scientists.

We may well ask, then: what is intelligence? In order properly to evaluate the nature of the inheritance of intelligence, it is first necessary to devise some method whereby intelligence may really be detected and measured.

Perhaps the most generally effective method

thus far devised for measuring or comparing intelligence is by a combination of tests for determining the so-called intelligence quotient (I.Q.). Such tests measure the skill of the subject in performing certain mental operations, involving, however, the use of words, numbers, and other symbols, as well as non-verbal experiences. Tests must be based at least partly on past experience, that is on learning. To some it may seem obvious that intelligence is acquired. Yet some individuals appear to have the nervous equipment for normal mental activity, even though it is not exercised, while others show little evidence of it despite the most prolonged exercise. It is the *ability* to learn that we wish to measure, above all, since it is this and not the learning itself which would be transmitted. Nevertheless, it is very difficult to separate the ability to learn from the measure of what has already been learned. If intelligence were purely acquired, we should expect all individuals with similar training to have similar intelligence. We know that this is not so. If intelligence tests were a measure of inherited ability only, we should expect all individuals with the same genetic constitution to achieve the same scores, as for instance, identical twins. Again this does not fully hold. Hence we must conclude that both environmental and hereditary factors influence intelligence, as it is now measured. A few samples of

TRAIT *	ONE-EGG TWINS	TWO-EGG TWINS (SAME SEX)	SIBLINGS, LIKE SEX
Difference in standing height	1.7 cm	4.4 cm	4.5 cm
Difference in weight	4.1 lbs	10 lbs	10.4 lbs
Difference in Binet intelligence quotient	5.9 IQ points	9.9	9.8
* H. H. Newman, F. N. Freeman & K. J. Holzinger, <i>Twins, A Study of Heredity and Environment</i> , University of Chicago Press, 1937.			

environmental and hereditary effects will allow us better to judge their relative importance.

One-Egg (Monozygotic) Twins

Nature has given us a well-nigh perfect opportunity to test the effects of different environmental influences on like genic complexes. Monozygotic twins result from the fertilization of a single egg by a single sperm, and they thus have an identical genotype, so that differences in growth, appearance, or behavior must stem wholly from environmental conditions. Such studies show a remarkable though expected similarity of the twins in physical structure, such as general appearance, height, weight, characteristic capillary structure, fingerprints, peculiarities in tooth formation, and brain waves, as recorded by the electroencephalograph. But even more significant is the fact that they usually develop similar diseases at about the same time, not only organic diseases, but also those due to bacterial infection, despite the differences in environment. And where one twin commits a crime, the other is likely to commit the same sort of crime. A study by Newman and others of 50 pairs of identical twins, 52 pairs of fraternal twins of like sex, and 52 pairs of sibs of the same sex, gives some measure of the relative effect of environment and heredity. The results

of this study are given in the table above. Clearly, identical twins show remarkable physical similarity in height and weight, and fraternal or two-egg twins, as might be expected, show not much more similarity than any pair of sibs of the same sex. For both fraternal twins and sibs share, on the average, one-half of those alleles for which their parents were heterozygous. In intelligence, identical twins usually vary no more in their scores than would the same individual on two different tests.

A further check on the relative effects of environment and heredity is obtained by comparing qualities of twins reared apart with those of twins reared together (see table below). Correlation here is expressed in terms of a computed coefficient, such that perfect correlation is indicated by "1" and a purely chance relationship by "o."

A high degree of correlation is shown in height, somewhat less in weight, and still less in I.Q. in one-egg twins reared apart. But it is notable that correlation between monozygotic twins reared apart is still greater than the correlation in two-egg twins reared together, suggesting that the effect of sharing only half instead of all the parents' genes has a slight edge over environment. In individual cases it is found that where one twin is bright, the other is usually also bright; but where one had better

	IDENTICALS REARED APART *	IDENTICALS REARED TOGETHER	LIKE-SEX FRATERNALS REARED TOGETHER
Standing height	.969	.932	.645
Weight	.886	.917	.631
Intelligence quotient	.670	.881	.631
* H. H. Newman, <i>et al.</i> , <i>op. cit.</i>			

schooling than the other, the former showed a higher I.Q.

In general, it has been found that whenever the one-egg twins had not grown up in very different cultural and educational environments, their I.Q.'s differed by five points or less. This is no more than two tests of the same person on different days; and alternate forms of the test frequently differ. But for a few pairs of one-egg twins, raised in very different circumstances, the I.Q. differences were much larger. The most extreme difference ever found was 13 points, between two twin girls, one of whom had only three years in grade school while the other had a college degree and teaching experience. On the whole, the average difference between identical twins reared together and reared apart is just about equal to the average difference between identical twins reared together and like-sex fraternal twins reared together. Average differences in the American environment affecting the I.Q. therefore have just about the same degree of effect as the difference between sharing all one's genes and only half one's genes with another person (the relevant genes being those for which either parent is heterozygous).

Are There Racial or National Intelligence Differences?

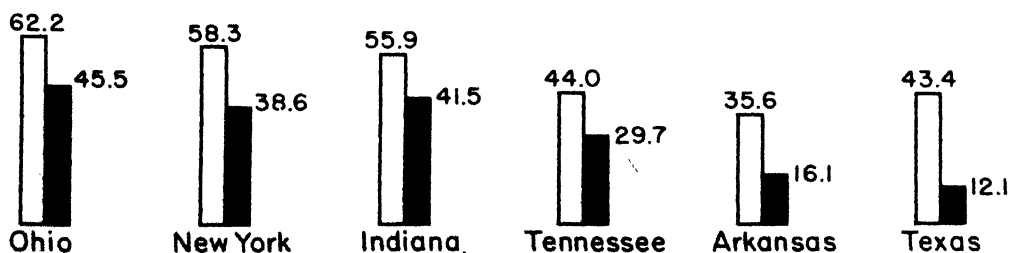
When American children of different national origins are tested for intelligence, group differences appear. In certain tests involving races and nationalities, the following scoring sequence, beginning with the highest, was obtained: Jewish, English, Norwegian, German, Japanese, Chinese, French, Finnish, Hungarian, Mexican, Italian. Before we accept such

evidence at face value, we may compare the performance of whites and Negroes as measured by certain army tests (Fig. 512). A glance at the scores of whites and Negroes in each state, shows that whites always rank above Negroes from the same state. Whites, we might then conclude, must be superior to Negroes. But we should also note that New York Negroes turned in a higher performance than the whites of any Southern state. Studies also show that the Negroes who migrate north experience a rapid rise in I.Q. It would be argued that the Negroes who emigrate north have a higher innate ability to begin with, but we have no evidence that this is so. Evidently then, environment plays an important role in establishing the intelligence rating as tested. Thus, until we can be assured that all those tested have had the same cultural and educational background and the same advantages, the claims of superiority of one nation, race, or people, over another are unjustifiable.

Occupations of Fathers and I.Q.'s of Children

Dull parents may beget bright children and intelligent parents may produce dull ones. Are such parent-child relations the rule, or are they exceptions? Are they due to genetic relationship, are they produced by the common factors in a family environment, or are they purely coincidental? In view of the complexity of what we call intelligence, and our ignorance of its determining factors, such questions are best answered statistically. We must examine not individual cases, but large groups of them. Such results, of course, yield probabilities, no more. With these facts in mind we may study the I.Q.'s of children, as related to the occu-

Fig. 512. Scores made by whites and Negroes in northern and southern states on the Army Alpha intelligence tests, given in First World War, 1917-18. Note that whites (white columns) in any one state always score higher than Negroes, but that New York Negroes score higher than any southern white group. What role does environment play?



OCCUPATION *	ORIGINAL FATHERS		FOSTER FATHERS
	LEGITIMATE	ILLEGITIMATE	
Professional	1	10	15
Semi-professional and business	2	16	41
Skilled labor	26	41	38
Semi-skilled to slightly skilled	34	28	5
Common labor	37	5	1
	100	100	100

* After Osborn, *Preface to Eugenics*, Harper, p. 84.

pational status of their fathers. In order to eliminate as far as possible the influence of differences in environment, children removed from the environment of the parents at an early age and placed in foster homes, or in institutions, are chosen as subjects. Two such groups of children were examined by Freeman, Holzinger, and Mitchell. Their fathers' occupations were distributed as shown in the table at the top of this page.

We see that 71 per cent (34 + 37) of the legitimate children were sired by fathers who were either semi-skilled or unskilled laborers, while of the illegitimate children, 67 per cent were sired by skilled laborers, semi-professional and business or professional men, that is doctors, lawyers, and others. Of the mothers of illegitimate children, 60 per cent had completed grammar school, but only 30 per cent of the legitimate mothers had. The children's foster homes, as judged by the occupations of the foster fathers, were better than average for the state of Illinois, but they were graded as good, average, and poor. The results are shown in the table at the bottom of this page. The table shows that the illegitimate children

ranked persistently higher than the legitimate in the same type of home. This result suggests that the presumably higher I Q.'s of the real fathers and mothers of the illegitimate children express themselves in the higher I Q.'s of their children. The effect of environment, on the other hand, is expressed by the higher I Q.'s of those children nurtured in the better homes. This was true both for the legitimate and the illegitimate children.

To contrast further the effect of a varied environment with that of a fairly uniform one, we turn to observations made by Lawrence in England. Two groups of children were compared. One was from the uniform environment of an orphanage (Dr. Smith's Home) for illegitimate children, where the children are entered below one year of age and are kept until the age of 15 or 16 years. The other was from a London elementary school to which children come from the different environments supplied by many homes (Figs. 513 and 514). In each school the children were classified according to the occupational class of the father as follows: Class A-B, tradesmen, clerks, highly skilled artisans, engine drivers, a few professional

FOSTER HOME *	LEGITIMATE		ILLEGITIMATE	
	NUMBER OF CHILDREN	MEAN I.Q.	NUMBER OF CHILDREN	MEAN I.Q.
Good	10	106.5	45	112.4
Average	19	98.3	39	104.9
Poor	16	83.4	27	95.6
	45	94.8	111	105.7

* After Osborn, *op. cit.*

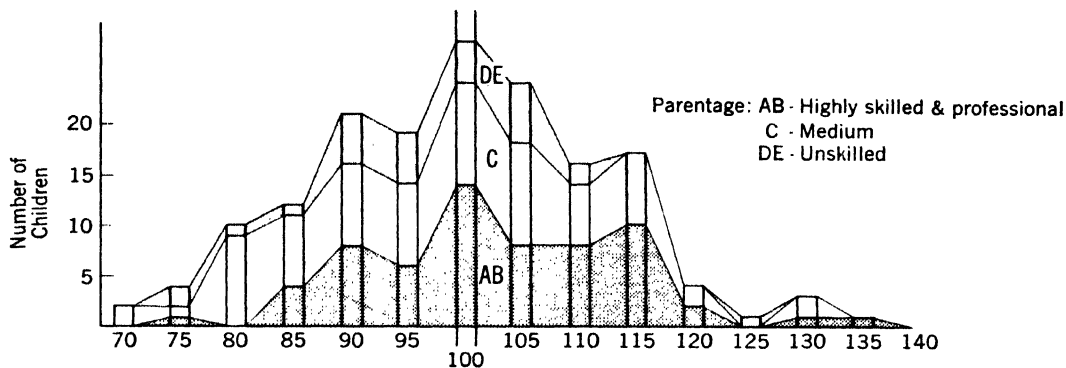
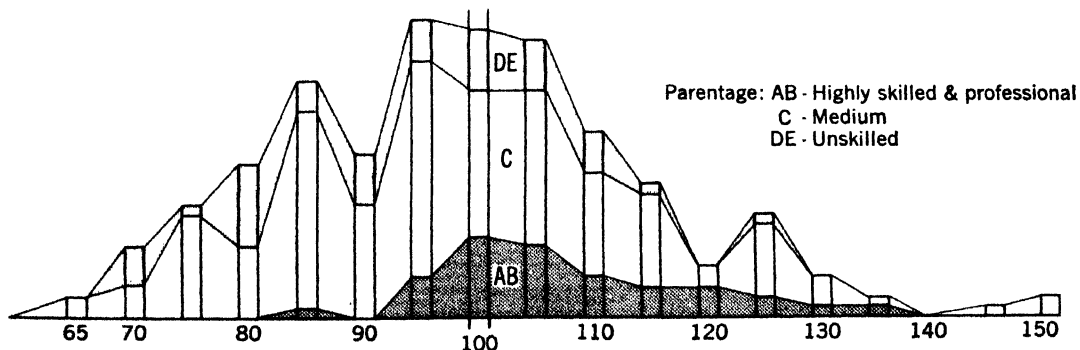


Fig. 513. The spread and distribution of intelligence in children in Dr. Smith's home, an orphanage, as classified according to occupational status of their fathers.

workers, and independent farmers. Class C, skilled and semi-skilled workers, such as bricklayers, bus drivers, police. Class D-E, unskilled or irregular workers, such as farmhands, dock laborers, street peddlers. The samples given involve only a few hundred individuals and hence are too small to yield final answers, but certain trends are apparent. The number of children of each class represented at a given I.Q. is indicated by superimposed columns. The areas connecting these columns give a measure of the relative contribution of each class to the various intelligence levels. Thus, in Dr. Smith's home, at I.Q. 75, there was one child of the AB group, one of the C group, and two of the DE group. First, note that the spread of intelligence covers about the same range for all classes in both schools, although there is a slightly greater spread in the London school. This suggests that a part of the spread

in the London school may be attributed to a more variable environment. The fact that all three classes of children, from A to E, range almost from one end of the chart to the other supports our statement that bright parents may have dull children. But note also that in both schools the bulk of the AB children falls on the upper side of the 100 I.Q. level, while the larger masses of both C and DE children are on the lower side. Since this shift is more evident in the children of the London school, we may suspect that the poor environment of the lower class homes has had a depressing effect on the children's I.Q.'s. Similarly, the better environmental influence of the AB homes may account for the fact that the AB children of the London school are shifted more to the plus side of the 100 I.Q. line. A look at the lower end of each school's distribution yields these figures: 15 out of the 16 children

Fig. 514. The spread and distribution of intelligence in children of a London elementary school, as classified according to occupational status of their fathers.



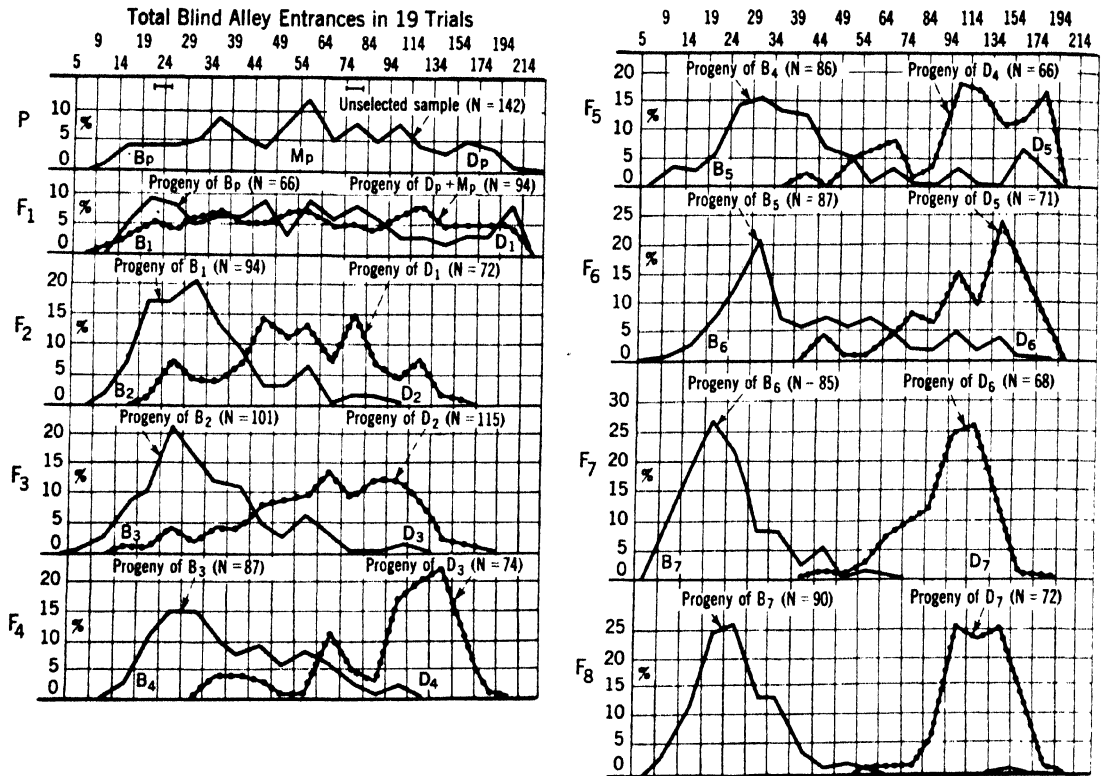


Fig. 515. Distribution of intelligence in selectively bred rats. By selecting bright rats (B) and mating these with each other, and dull rats (D) and inbreeding those within each group, two genetically differentiated groups of rats were produced from a mixed population in eight generations.

in Dr. Smith's home with 80 I.Q. or below derive from C and DE fathers, while all 33 children in this I.Q. range in the London school came from these lower classes, and the AB group contributed none. The study may be summed up by saying that a good environment appears to elevate the I.Q.'s of children, and a poor one depresses them; and that there is a statistical correlation between occupational status of fathers and the I.Q.'s of children. Since occupational status alone can scarcely be expected to be strictly on the basis of intelligence, and in any case only the male parent has been considered, we might expect these trends to be more pronounced if both parents' actual I.Q.'s had been known.

Linking these observations with what we know about the mechanism of heredity, we would suspect that intelligence is controlled by

many genes working in various still unknown correlations, and that the average person is quite heterozygous for intelligence-controlling genes. In this manner we can account for the occasional dull children of bright parents. In the process of segregation such children simply received a relatively poor selection from the better average of each of the two parents. Had the parents been nearly or quite homozygous for those genes favoring high intelligence, no such thing could be expected to happen. If this assumption is correct, it should be possible to attain a degree of "purity" (homozygosity) for either "bright genes" or "dull" ones, by a program of selective breeding. So far as human kind is concerned, this must remain merely a theoretical possibility, at least for the present, but an answer should be forthcoming from animal experimentation.

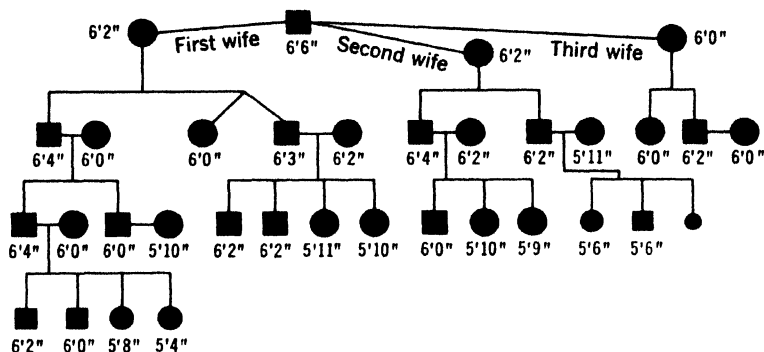


Fig. 516. Pedigrees of three families showing assortative mating and inheritance of stature.

Heredity of Intelligence in Rats

A recent study on the selective breeding of rats by Tyron yielded illuminating results. A random sample of rats was carefully tested for individual ability to learn to run a maze. The number of blind alley entrances, that is, false turns, made by each rat in 19 trials while learning to run a maze served as a measure of its "maze-intelligence." This varied over a wide range, from very bright to very dull (Fig. 515). By mating bright individuals with each other and also by mating dull to dull, an almost complete separation into two intelligence groups was achieved in only eight generations. The graphs plotted on the basis of these experiments show several additional features of interest. First, nothing new appears to have been added or created by this assortative mating, for the range of intelligence in the unselected parent stock was just about as great as it was at the end of the experiment. Second, even in the F_8 generation there was overlapping; that is, the brightest of the dull line were brighter than the dullest of the bright line! But the total shift in intelligence is impressive, for in the F_8 bright group over 50 per cent of the population had an intelligence rating (24 errors) which was matched by only 10 per cent of the parent stock. Thus although top performance was not raised, the average performance (*i.e.*, intelligence) of the F_8 bright stock was raised enormously. It is as though the average human I.Q. had been raised, say, from 100 to 140 in a mere eight generations. But we must not ignore the dull side, for here too things have been happening. In the same eight generations, 50 per cent

of the dull population achieved a degree of dullness attained by only about 20 per cent of the unselected parent stock. Thus although selective breeding appears to produce no outstanding individuals, either in one direction or the other, it has a profound influence on the collective intelligence of the group.

If all kinds of people mated at random and manifested equal fecundity, we would expect each succeeding generation to exhibit about the same range and relative proportion of all human types. But do people mate at random, and do they reproduce at the same rate? We may suspect so, from personal observation, but statistical samples serve as a sounder basis for such conclusions. In other words, is there *assortative mating*, and are there *differential birth-rates* for groups or classes with different characteristics?

OTHER GENETIC FACTORS

Assortative Mating in Man

Statistics show that there is a tendency for tall men to marry tall women and short men short ones. In a study of Davenport of 54 very tall men, 49 of them married women above medium stature, whereas of 63 very short men, only 12 selected women above medium stature. An item perhaps irrelevant, but of interest, is that short men are more likely to marry tall women than tall men are to marry short ones. That such assortative matings produce correspondingly tall or short children is shown by the pedigrees in Figure 516.

It is doubtful if assortative mating plays a major role in man for most physical qualities.

It is known of course that members of the same race or religion are more likely to find mates within their group than out of it, but this may be due largely to social propinquity. We do, however, have statistical evidence concerning assortative mating with regard to intelligence and social status. In the data previously presented regarding legitimate and illegitimate children in foster homes, it may be recalled that the mothers of the legitimate group of children, sired largely by fathers in the lower occupational groups, had a lower average educational attainment than the mothers of the children whose fathers were of higher occupational groups. And we find that parents of intelligence produce, on the average, children with higher intelligence ratings. But all of this assortative mating, together with a degree of inheritance of intellectual ability, should have little effect on the average intelligence of the next generation unless some selective factor operates. In the case of the maze-running rats, the selective factor was clear-cut and sharp — it was simply the choice of the experimenter himself. Are there, then, any selective factors operating upon the human species besides those causing the immediate removal of genic complexes which are wholly inviable?

Differential Birthrates

Ultimately, the rate of increase of any population group is determined by the relative magnitudes of the birth rate and the mortality rate. If the number of children that reach the reproductive age before dying is increasing, then the population will increase at an accelerating rate, even though the individual fertility rate remains the same. Thus in comparing the rates of growth of groups or populations with different living conditions, it is necessary to compare their net reproduction rates rather than their gross reproduction rates. The gross reproduction rate states merely the number of daughters born to each woman of reproductive age. The net reproduction rate takes into consideration the mortality rate and is so computed that "1" represents a static population level. Where statistical information is limited, the number of

children under five years of age per woman of child-bearing age may serve as an indicator of the net reproduction rate. Where conditions are such that mortality rates may be assumed to be similar for the groups to be compared, gross reproduction rates may serve for comparison. Improved medical facilities for all classes are gradually bringing mortality rates in civilized communities to more nearly the same level.

The World Population

Civilization has brought with it a decline in mortality rates as well as a decline in fertility, with the result that the net reproductive rates in many civilized countries have dropped below 1, that is, below the bare replacement level. There is nothing very ominous about this fact, for the population pressure in many parts of the world has become excessive, and standards of living have become greatly depressed. It must be considered quite ominous, however, that populations appear to increase in inverse proportion to their cultural level, especially when modern medical methods are introduced to backward populations.

India is perhaps the most dreadful example, for here the bulk of the population lives on a subminimal subsistence level. The average Indian today gets 960 calories a day, and undernourishment is considered to begin at 2000 calories by our standards! Although India is 90 per cent agricultural, 3,000,000 people died of starvation there in 1943. Over 25 per cent of Indian babies do not reach their second birthday, and only 42.7 per cent of all females survive to the thirtieth year. Despite this, the fertility of India is so excessive that the population has increased by 83 millions in the last 20 years, and is expected to increase another 83 million in the next ten years! While this is happening in unhappy India, and to a less degree in many other parts of Asia, populations in the most highly cultured nations are static or declining. The differences of net reproduction rate are striking, and population growth in Asia will eventually affect every other nation in the world.

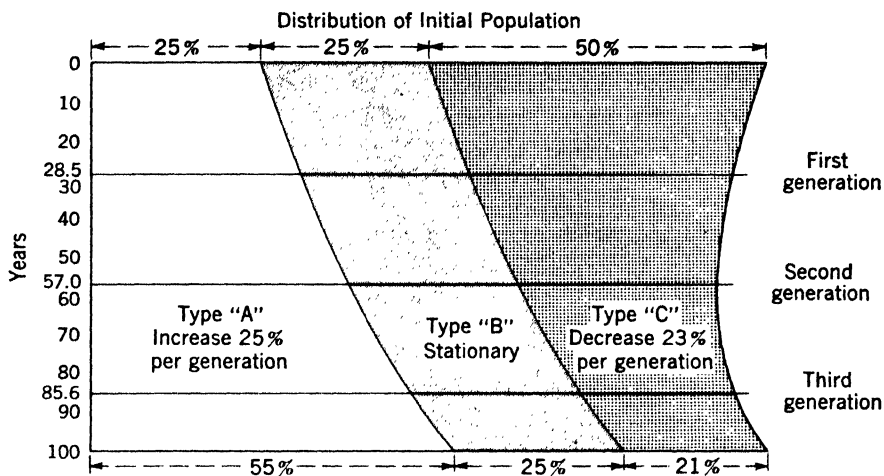


Fig. 517. What happens within a population composed of groups with differential birthrates. In the United States, the old native stock behaves somewhat like B and C. New immigrant stock and non-white stock approaches the pattern of type A.

Differential Birthrates, United States and England

The net reproductive rate of a country such as the United States is a composite of the reproductive rates of many subgroups, each with its own reproductive rate. It is quite evident that the composition and average reproductive rate of the country must change as a result of different group rates (Fig. 517). For example, the net reproductive rate of Negroes, Mexicans, and foreign-born whites is about 20 per cent higher than that of native whites, and we must thus expect a gradual partial replacement of native stock by the faster reproducing ones. But this shift in national composition is not so important unless it also implies a shift in the general level of intelligence, health, or other paramount qualities. Continuance of the democratic form of life, or ultimately of any culture at all, depends upon a sufficiently high average intelligence of the whole population. Fortunately, intelligence appears to be limited by no racial or national barriers.

The obvious method of determining whether there is any significant correlation between intelligence and reproductive rate would be to measure individually the intelligence of a number of children of couples with measured I.Q.'s. Such measurements have been made, but since they are difficult and expensive to

obtain in sufficiently large numbers, other correlations have been established and are often substituted. Such correlations may then be checked against each other. Thus, it has been found that groups representing higher occupational levels also have higher I.Q.'s, more schooling, greater income, and more expensive homes. (Remember, correlation does not imply cause and effect. It means only that for some reason an association exists.) That there is some correlation between these factors appears evident, but whether the I.Q. is higher because of the better education, or vice versa, or whether both vary together because of some other factor, we cannot say. The answer is equivocal, for we know that I.Q.'s can be raised by better training, but we also know that low I.Q.'s generally terminate formal education at low levels. And what of the correlation between I.Q.'s and occupation? Here there may be marked differences of opportunity, but when a mature man remains an unskilled laborer or farmhand, despite educational opportunities such as those available in this country and in England today, the assumption of low I.Q. is usually justified. Furthermore, it is supported by the depressed I.Q.'s of their children, even when these are raised in the uniform environment of an orphanage or the improved environment of a foster home. And since, under reasonably

normal conditions, income rises from unskilled to skilled to professional workers, a correlation between education, occupation, income, and value of home may be expected, with perhaps minor exceptions, as in the case of teachers and social workers. On the basis of these assumptions, let us then examine groups classified according to these categories.

Fertility and Income

We may compare the number of live births during one year per 1000 women between the ages of 15 and 44, in six income classes, distinguishing two groups in each class: 1. the married women, and 2. all women (Fig. 518). The distinction is important, since it gives additional information on the causes contributing to the differential birthrate. First, there is a steady drop in fertility from the lowest socio-economic group to the highest. There is, furthermore, a clear reversal in the ratio of fertility between all women and married women only, from low income groups to high. Where in the lower groups the fertility rate for all women is higher than for married women alone, indicative of a very substantial crop of illegitimate children, the relationship is reversed in the higher income groups. Here we find many independent, unmarried and childless women. Women on relief produced three times as many

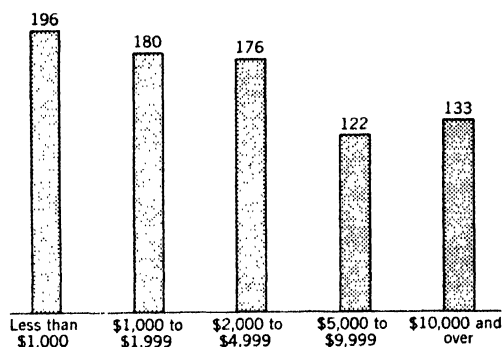


Fig. 519. Children per native wife in the east North-Central United States in relation to value of home. Note the slight increase in number of children in the most expensive homes. Such a change appears to be deliberate in response to lightening of economic burden.

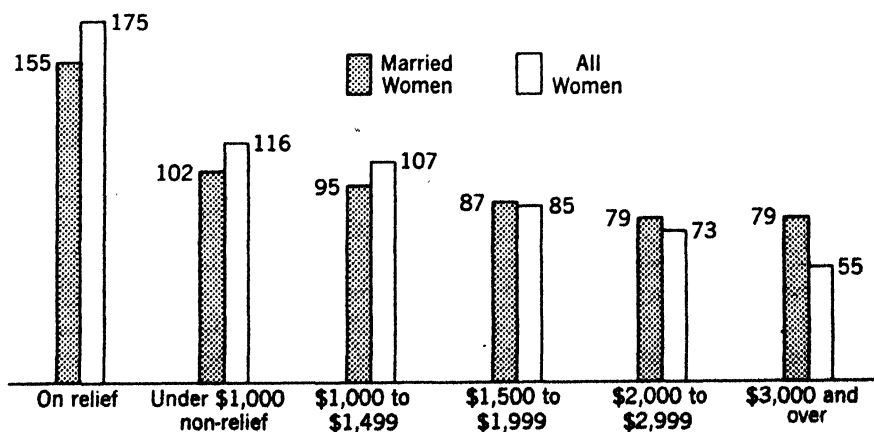
children as those in the \$3000 and over income class.¹

Fertility and Home Value

In another study, the fertility was measured in terms of children per 100 wives, and although fertility again shows a decline as we go from lowest cost homes upward, there is a reversal in those wives living in the most expensive homes

¹ Since these statistics are for 1935, in the years of the depression, fertility rates in the higher income groups, where birth control is usually practiced, must be considered to be especially depressed.

Fig. 518. Ratios of fertility in various income classes. Note the shift between married women and all women in each class as income rises.



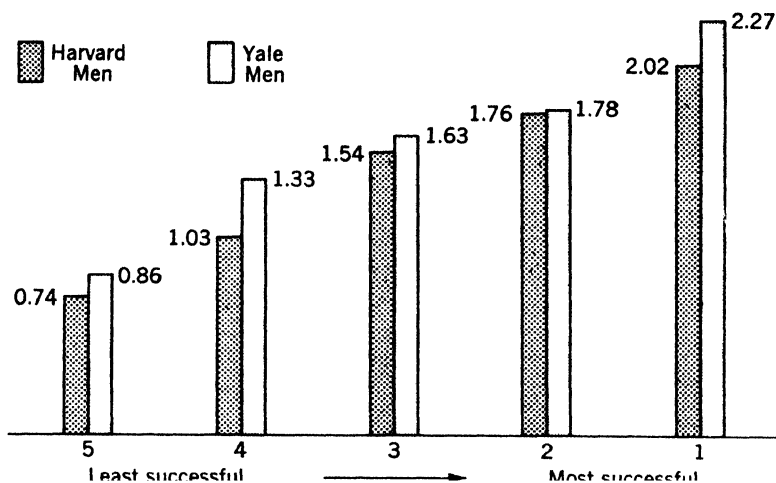


Fig. 520. Average number of children per college man according to business success. Here the fertility trend is reversed, and follows the pattern hinted at in Fig. 519. Yale men appear to be more fertile, while Harvard lags slightly.

(Fig. 519). The reason is not very difficult to guess. These families, like the group immediately below them, practice birth control and thus determine their family size. Being freer of economic pressure, a few additional children are deliberately planned.¹

Fertility and Business Success (College Graduates)

In a study of the number of children per college man, the latter classified according to "business success," we find a complete reversal of the fertility trend for the general population (Fig. 520), except that indicated in the highest category of home values. Although all of these

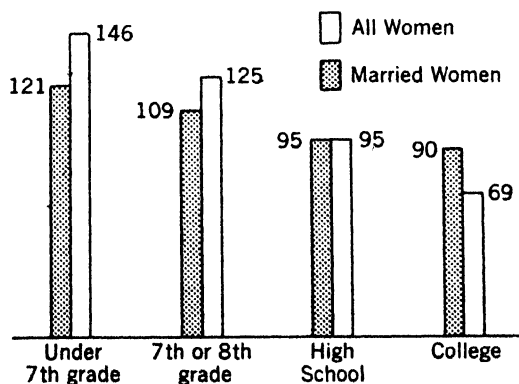
¹A few notes on birth control may be helpful. Among "very poor" whites, 30 per cent of the women attempt contraception, among the "moderate" 38.4 per cent, but among the "well-to-do and rich" fully 80 per cent. The pregnancy rate of all women practicing contraception is lowered 24 per cent below that of the non-contraceptive group, but among the "very poor" it is lowered only 12 per cent, whereas among the "rich" it is lowered 44 per cent. The latter figure must not be considered indicative of the absolute efficiency of contraception, for many of these women make use of contraception merely for the purpose of properly spacing their children. Regardless of its effectiveness the widespread practice of contraception is evident from the fact that the contraceptive business grossed over \$250 million in 1937 — or nearly as much as the jewelry business.

college men (except possibly the most successful Yale men) reproduce below the replacement level, the most successful have almost three times as many children as the least successful. Again, as in the preceding group, the reason seems rather obvious. Birth control is of course practiced in all these groups, and economic pressure therefore largely determines the size of the planned family. If this principle were applied to the entire population it would be considered of definite eugenic value.

Fertility and Educational Attainment

As we found a correlation between fertility of women and their economic class, so we find

Fig. 521. Relative ratios of fertility according to educational attainments. Compare this with Fig. 518.



a similar correlation between fertility and educational attainment (Fig. 521).¹ Poor education, like low income, is associated with high fertility; whereas good education, like high income, is associated with low fertility. In the United States, educational attainment, at least through high school, is determined to a large degree by innate capacity rather than by economic conditions, and educational attainment is thus to a certain degree correlated with intellectual ability.

Family Size and I.Q.'s of Children

When a group of Chicago children examined at the Institute for Juvenile Research was classified according to I.Q., the results showed that those with the highest scores had fewer brothers and sisters than those with the lowest. In other words, there was a correlation between family size, or fertility, and the intelligence of the children, and presumably of the parents. The highest reproduction rate, measured in terms of the average number of children per family, appeared in the high grade moron or lower borderline groups. At both ends, in the feeble-minded as in the families of gifted children, a lower reproductive rate was found to prevail.

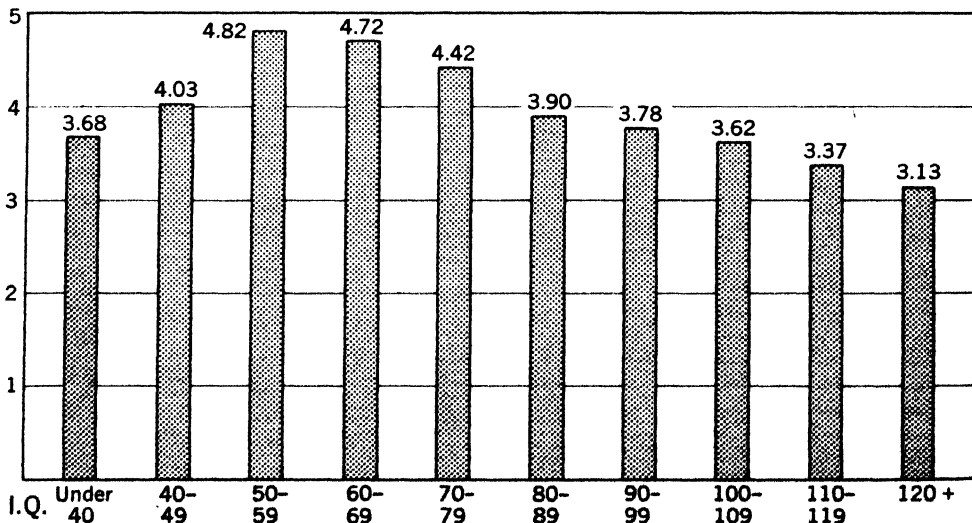
¹ In both cases fertility of married women and of all women is expressed in live births per 1000 women in the reproductive age.

But even in the lowest intelligence group — under 40 I.Q. — the number of children per family exceeded that in the highest I.Q. group of 120 or over.

Intelligence Groups and Total Population

Drawing our information from a tabulation of distribution of London school population over the I.Q. scale made by Cyril Burt (1946), we obtain the relationship shown in Figure 523. Out of a random sample of 100 families, only 2.7 produce children with an I.Q. of 130 or above. Since the average number of children produced by such families is relatively low (only 2.3), only 1.8 out of a random assortment of 100 school children fall into this class. Looking at the low side of the I.Q. range, we find that children with an I.Q. under 70 are derived from 1.1 per cent of all families, but since these are relatively fertile, with 4.7 children per family, they contribute 1.5 per cent of all school children. Simple calculations show that if all families had the same rate of reproduction, then the average I.Q., instead of being 100, would be 101.9. The differential birthrate then appears to result in a decline of 1.9 points in the I.Q. scale. Similar studies by other investigators show similar results. Some show lower, some higher I.Q. loss, but all indicate a loss.

Fig. 522. Family size in relation to I.Q.'s of children. Note the decline in fertility rate of the feeble-minded and low morons, whose fertility rate still exceeds that for families with superior children. Note that the highest reproduction rate lies in the high-grade moron level.



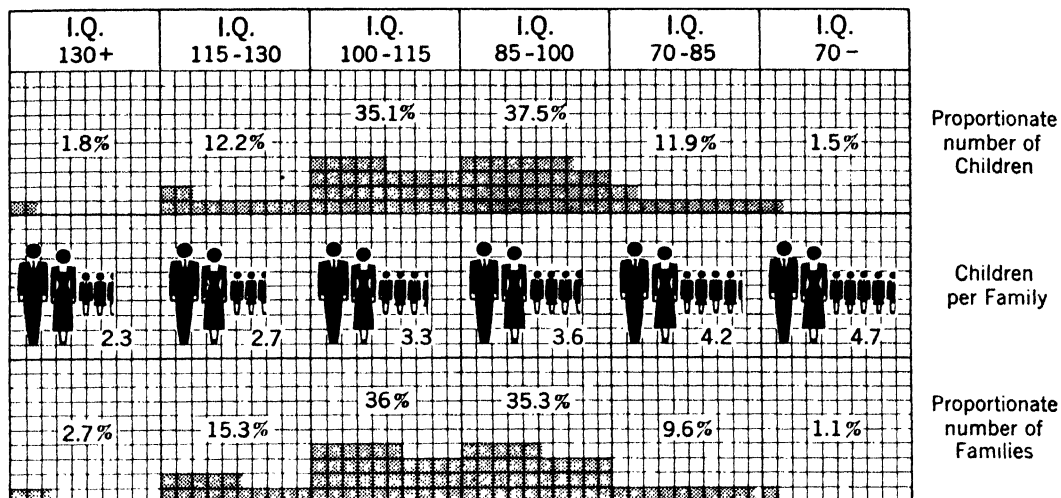


Fig. 523. Total contribution of intelligence groups to total population. The percentages above indicate the average number of children in the families whose children are at the I.Q. level indicated. The percentages below give the proportion of families in that group. Note that the greatest contribution comes in the groups on the wrong side of the 100 mark.

Differential Birthrate and Later Generations

Does the differential birthrate with respect to innate intelligence make a decline in the average intelligence from generation to generation inevitable? Many investigators think so, and numerous predictions as to the future distribution of intelligence in the general population have been attempted. Using the estimated distribution of school populations with respect to I.Q. compiled by Burt, we might expect a change somewhat as shown in Figure 524 during the next fifty years. Here the "cream" of innate ability shows a slight but nonetheless alarming decrease, with a consequent increase of the "skim-milk" at the bottom. According to these estimates, in fifty years the superior individuals will be only half as numerous as today, while those of "moron" caliber will have doubled.

EUGENICS AND THE FUTURE

Where Are We Going?

The tables and charts compiled from the studies of human intelligence present an ominous picture of decline. To the student of organic evolution this is scarcely startling; in-

deed, not so much as a gain would be. For man has evolved to his present estate through the hard school of natural selection. Some evolutionists have interpreted this to mean that ruthlessness, aggressiveness, cruelty, and deceptiveness are inherent in man's nature and in his successful evolutionary rise. But this is a biased view, for those qualities we admire more, and upon which modern culture is based — charity, tolerance, compassion, mercy, co-operativeness — may be equally inherent and necessary to man's survival and success. Man is a social animal. That is, social groups have had higher survival value than solitary types. Natural selection has operated to preserve and strengthen those qualities essential for the success of groups as well as those essential for the success of individuals. First, the family; then, the tribe; still later, the civilized society of a nation or group of nations — ultimately, if we are to survive, worldwide cooperation and unity. It cannot be doubted that natural selection has shaped man of both these ill-fused sorts of qualities, the ruthless and the kind, the inimical and the cooperative, but, it would seem, predominantly of the social qualities. Our hope lies in the refined metal of heart and

head; our peril in the feet of clay.

Yet our very compassion and mercy may work against us, in a eugenic way. The preservation of every defective genetic type and its allowance to propagate, by weakening the rigor of natural selection, increases the frequency of undesirable genes in the population and necessitates in every generation a greater load of surgical patchwork, medical attention, and institutional care. For example, diabetes is no longer commonly fatal. The gene responsible for diabetes may be expected now to increase in frequency to a considerable degree. This will mean, in a generation or two, a considerably larger number of diabetics who will have to go through life dependent upon the administration of insulin. This is doubtless a golden prospect for the manufacturers of drugs, but is it a hopeful prospect for society as a whole?

We have observed that man, more than any other creature, has wrought profound changes in his own environment. He has changed the stream bed in which his germ plasm flows, and thus he has changed his future and his goal. Man has just discovered that this is so, and realized that in the past he was a product of blind evolution; now he is on the verge of discovering how to direct his evolution consciously. Indeed, he must do so, or pay the penalty for his heedless modifications of his environment's selective actions.

That the qualities which constitute man have a genetic basis cannot be questioned. They are modifiable, however, if within strictly limited boundaries, and no one will question that they should be modified as favorably as possible. The problem is to know just what really is favorable. Any race or group can and should be improved by eutenic measures, that is, by better education, housing, and feeding. But the evidence is now incontrovertible that, as with other creatures, any human quality for which the selective factor is removed will in time deteriorate. The modern culture of man has removed many selective factors.

Medicine has removed many of those for innate disease resistance as well as for normal physical and mental structure. We approve,

or at least accept, some of the changes that inevitably follow. Physically, future man may show less sexual differentiation in build, to the extent that Caesarian operations remove the selective value of a broad female pelvis, and that improved bottle formulas for infant feeding largely remove the selective value of the female breast. Thus we glimpse the human female of the future as flat chested and narrow-hipped, a far cry from the "pin-up." Future man may well be toothless, and future embryologists may view the embryonic tooth-buds that never erupt with the same interest we now find in the embryonic tail. Our distant descendants may then note with revulsion that their ancestors once actually had teeth, exactly like animals! Such values can and do change, and we are hardly qualified to denote them either good or bad.

Again, digestive tracts may dwindle, if prepared liquids become the ideal if not the only food. Toes may fuse and the hair of the head may follow body hair into limbo. We may, perhaps, visualize all future babies as being delivered early and artificially incubated, and perhaps all of them will be subject to a series of surgical operations and patchwork, and to numerous serum injections, before they become capable of surviving at all.

The really objective student will not be repelled by this picture of the physical characteristics of future man, but he will still regard as decidedly ominous the signal of declining intelligence. For mind there can be no substitute, and without it civilization, and perhaps man himself, cannot survive. Even now, the problem of substituting reason for violence in settling international disputes appears to be practically beyond the power of our present level of intelligence. What would happen if this were lowered?

The inferior deviates, those with an I.Q. below 70, even now constitute 2 per cent of the population. It is estimated that in 1930 there were 850,000 feeble-minded children of school age in the United States, and another five million are just above the range of feeble-mindedness! Some will argue that education has been

shown capable of elevating I.Q. levels, and that is true, to a certain extent. Indeed, improved education could conceivably elevate the I.Q. faster than the dysgenic differential birth-rate might depress it. But this could not continue indefinitely. The day of reckoning would be merely postponed.

What Eugenics Is

To the average man the term eugenics perhaps still connotes the theoretical and impractical attempts of science fiction to create a superhuman race. In its modern aspect, practical eugenics is neither more nor less exciting than embryology, paleontology, or genetics. It is not spectacular and promises no immediate spectacular results. True, it is the science that concerns itself with race improvement through breeding, but in actual practice, at least for the present, it is primarily concerned with preventing race deterioration. That there is a vital need for such measures can no longer be questioned by any competent person. The problem is immensely difficult, for two distinct reasons. First, we still know far too little about human genetics; and second, human germ plasm is housed in highly refractory, individual packages, and measures that would be entirely satisfactory from the viewpoint of genetics may be wholly impractical psychologically or sociologically.

The statistics presented in earlier pages hold much hope, and point the way to practical and conservative approaches to eugenics. Modern medicine offers practical tools for such measures. Few will dissent from the view that congenital idiots, such as those shown in Fig. 509, should not be permitted to propagate. Fortunately relatively few of them do, but we can make certain that they do not by providing for their sterilization. Modern methods of sterilization must not be confused with castration or emasculation, and in no sense should sterilization be construed as a punishment. The intelligent and conscientious individual who considers himself a possible carrier of Huntington's chorea, schizophrenia, hemophilia, or a similar affliction, will welcome the guarantee that he

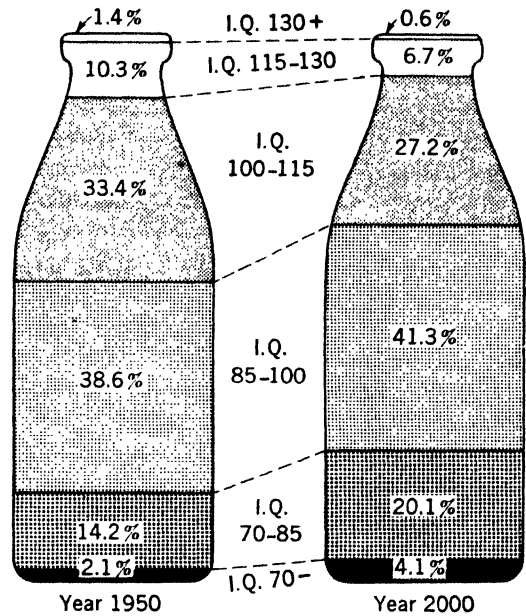


Fig. 524. An estimate of the probable dilution of intelligence during the next fifty years. After Cyril Burt, *Intelligence and Fertility*, Eugenics Society (London, 1946), page 32.

will not find himself in the position of passing on such conditions to the next generation. Clearly, the responsibility of deciding who is to be sterilized is a heavy one, but perhaps less so than the decision of judge and jury in condemning a man to execution or life in prison.

Possible Eugenic Measures

With this the question has been broached: should it be possible to prohibit the procreation of an individual by law? Since it would be insanity, in the light of present-day knowledge, to permit known congenital idiots or insane persons to propagate, the choice to be made lies only between segregation and sterilization. In actual practice, the lack of sufficient facilities results in the release of many individuals segregated for a time, with the frequent result that many return for care, along with their offspring. Sterilization laws have been passed in 29 states in the United States, and it is an accepted practice in many countries. Up to

January 1, 1940, about 33,000 individuals were sterilized in this country, about half of whom were insane and the other half feeble-minded. California leads the list, with over 14,000 sterilizations. But, not all states consider sterilization legal, and among them are such populous states as New York. Here the propagation of feeble-minded and insane continues unchecked.

But sterilization and segregation of the grossly unfit will have little or no influence on the shifting level of intelligence that results from differential birthrates. That the latter are not due to inherent differences in fertility appears quite certain, for in states in which birth-control clinics are active, the birthrates of the lower socio-economic classes have dropped — a clear indication of what is virtually self-evident, that the high birthrates in these classes are due to helplessness and ignorance and not to any greater desire to procreate. Workers at public clinics are depressingly aware of their patients' lament over too-frequent pregnancies, and of the failure of these same women to make adequate use of services designed to help them; but their wish to do so cannot be questioned. Birth control as a means of spacing children and adjusting their number to the means and desires of the parents now has legal status in all but two states in this country, the exceptions being Connecticut and Massachusetts, where it is considered illegal for a physician to impart information regarding birth control to a married woman under any circumstances. Medical abortions, however, are sanctioned.

Birth control alone, however, will not remedy the misbalance in our reproductive rates, for contraception is already generally practiced to the greatest extent by the higher socio-economic classes, and it can serve only to lower the reproductive rate of the lower classes. Furthermore, many European nations, and recently the United States too, are confronted with the threat of a national decline in population as the result of a net reproduction rate below the maintenance level. Racial and national patriotism is still strong enough so that this condition is viewed with alarm, indeed with more alarm than the less obvious and

much more ominous decline in the level of intelligence. The numerous devices used by various countries to increase fertility are quite well known. In 1945, 31 countries had introduced family allowances. Marriage loans with rebates for every child, bonus payments, automatic raises in salary computed on the number of children, public acclaim and honorary medals bestowed on women with great numbers of children, all of these have been employed, but all are looked upon with a jaundiced eye by the geneticist, for they are predominantly dysgenic in effect. Bonus payments, loans, and subsidies are but slight inducements to the higher socio-economic group, for the greater cost of rearing a child at a high standard of living is not balanced by the grants. In the lower income groups the cost of raising a child is far less, and under some circumstances the child may even be considered an asset, so that here subsidized procreation may become a lucrative sideline. Such measures, though they may be effective in raising national reproduction — note Germany's rise in reproduction rate from .70 in 1933 to .945 in 1938 — are likely to cause a still greater drop in the I.Q.

Are there then no methods by which this situation can be righted? Were human beings docile animals, the answer would be relatively simple, as witness the rat-maze experiments. But personal freedom must be maintained in so far as it is possible in a civilized and interdependent community.

The Scandinavian countries, and particularly Sweden, have been the most progressive states in attacking this problem. Their experience indicates that a sharing of the burden of child-raising by the state, that is, by all the people, not by means of money grants but by free meals and free education, appears to have a stimulating effect on the reproduction of the middle and upper classes, while it appears to have little effect of any sort, on the lower. This seems logical, for the voluntary curbing of childbearing results from a deliberate decision, based partly on selfish motives but partly on a deep sense of responsibility to provide adequately for the rearing of the child. The cost

of rearing a child to the age of 18 in the United States has recently been estimated to vary between \$12,000 and \$20,000, depending on the socio-economic class. Clearly, it would be much lower than this for the lowest classes. The apprehension of such a cost causes considerable deliberation before thinking individuals permit themselves to have children. But if such people knew in advance that all schooling and all meals during school attendance were to be furnished by the state, to be paid by money contributed by all (including especially the childless, married or unmarried), many would then be inclined to have more children. Such a transfer of the cost of rearing children to those who have none of their own may be defended on the principle that the present generation owes its culture and its existence to its forebears, and every member of this generation owes a similar debt to the future.

But there are still further discriminations with dysgenic effects. Even in a country where education is free to all capable of accepting it, those most gifted intellectually, and thus training for the professions, can hardly expect to be self-supporting before the age of 30, while those remaining in the unskilled or semi-skilled classes may marry and have children at twenty. To word the situation slightly differently: is it fair to penalize the intellectually superior individual training for a profession, by denying him the right to marry at the normal marrying age? And is it fair to the race itself to depress the reproductive rate of this class of individuals by so shortening their procreative period? The idea of paying a gifted individual while preparing himself for a profession finds clear expression in the G.I. bill of rights. An extension of such measures, based strictly upon ability, would have decided eugenic effects.

Still, the dice are loaded against the procreation of those with higher I.Q.'s. The intellectual woman often finds that marriage would seriously hamper her career, for a number of reasons. What an irreplaceable loss that over 50 per cent of the graduates of our finest women's colleges never marry, and that the percentage is even higher among graduate stu-

dents, the intellectual cream of the crop!

Conclusions

Detailed studies of differential birthrates rightly belong in the field of sociology. The foundations of all such deliberations must be built, however, by the geneticist, and any sociological solution must rest upon his findings.

Evolution has produced in man an astounding and unique organism. Its future potentialities exceed even the ken of this most imaginative of creatures. We need but extend the curve of progress from ape-like progenitors to man an equal interval of time into the future to see the most dazzling possibilities. And these would still be but a beginning. Life itself has existed only 2000 million years. With luck it may exist as long again. At most, 1/1000 part of this has seen man rise above the animal level. He may proceed a thousand times as far again! Even as his mental plane is new, so his descendants may achieve some intellectual miracle on a plane as far beyond our comprehension as is ours beyond that of *Amphioxus*.

But these dazzling prospects are not guaranteed. Man's upward evolution appears to have hit a snag. Not only has it stopped, but it appears to have gone into reverse. As we ponder the charts, we are reminded of the tunicates, perhaps, and wonder whether man may have met an obstacle insurmountable for the species, though the solution is clear to that small percentage of the human race willing and eager to see. And so we sense two essentially different paths leading into the future. Along one, the way of *laissez-faire*, we are now idly strolling, scarcely noting its easy decline. The other path does not yet exist. We must build it as we go, step by step, and the heights which we may thus scale are proportional to the wisdom with which we build. The first few steps have been constructed or designed by an intellectual minority. Time only will tell whether the mass of humankind will turn to assist in the task, or whether, in blind and uncomprehending rage, they will tear down what appears to them only a barrier to their comfortable journey downward to extinction.

APPENDIXES

A. CLASSIFICATION OF PLANTS AND ANIMALS

B. BIOLOGICAL TERMS



Classification of Plants and Animals

Without some orderly cataloguing of the approximately one million species of plant and animal organisms, any attempt to understand their relationships would be hopeless. Although sharp segregation of groups is not possible, certain natural groupings do stand out rather clearly, and in most cases there is little doubt about affiliations. Since the widespread acceptance of the concept of evolution, organisms are classified essentially on the basis of their relationships. Modern classification, then, is more than an arbitrary pigeonholing of organisms; it is to a considerable extent a tabulation of relationships, though distorted by the fact that the evolutionary pattern is that of a much branched bush rather than the ladder-like one necessarily employed in these pages. Although it cannot be said that a preceding group is ancestral to a following one, the preceding one is generally the more primitive and the closer to even more primitive ancestral forms.

Kingdom PLANTAE (350,000)¹

Plants usually have rigid cellulose cell walls and in general show less mobility than animals. Nutrition is usually autotrophic, though it may be saprophytic or parasitic. The animal and plant kingdoms overlap.

PHYLUM SCHIZOPHYTA (5000) (Gr. *schizein* = split + *phylon* = plant) The simplest of all plants without sharp differentiation of nucleus. Reproduction asexual, by splitting. Few general plant characteristics.

CLASS BACTERIA (SCHIZOMYCETES) (Gr. *mycelos* = fungus) Cells small and of varied shapes, often in characteristic clusters or chains. Many motile, some flagellate. Colorless or pigmented; no chlorophyll. *Nitrobacter*, *Azotobacter*.

CLASS CYANOPHYCEAE (Gr. *kyanos* = dark blue substance) The blue-green algae, simplest of green plants, considered primitive survivors of ancient line. Often form long filaments. Sometimes found in hot springs. *Oscillatoria*, *Nostoc*.

¹ Figures in parentheses indicate approximate numbers of species.

PHYLUM THALLOPHYTA (100,000) (Gr. *thallus* = a young shoot) Simple, relatively undifferentiated; consist usually of a thallus without true leaves, stems, or roots. Unicellular, colonial, or multicellular; with or without chlorophyll or similar pigmentation. Cells distinctly nucleated. Usually some form of sexual reproduction, but no regular alternation of generations.

Subphylum ALGAE (L. *alga* = seaweed) Autotrophic thallophytes with chlorophyll.

CLASS FLAGELLATA (L. *flagellum* = whip) Possible archetypes of primitive animals as well as plants. Single-celled or colonial, with one flagellum. Some have chlorophyll and are holophytic, some are colorless and are frequently classified as Protozoa. *Euglena viridis*; *Trypanosoma gambiense*.

CLASS CHLOROPHYCEAE (Gr. *chloros* = light yellow-green) Green algae. Chlorophyll in special bodies called chloroplasts. A heterogeneous group of nine orders.

Order Volvocales (L. *volvare* = to roll) Microscopic single-celled plants, sometimes colonial, often with two or more whip-like cilia. Show all stages from simplest sexual reproduction to full differentiation of sex, and from single-celled to almost multicellular. *Sphaerella*, *Chlamydomonas*, *Pandorina*, *Eudorina*, *Pleodorina*, *Volvax*.

Order Chlorococcales (Gr. *chloros* = yellow + *kokkos* = seed) Simple, spherical green cells, some on land, some aquatic, some symbiotic. *Pleurococcus*, on tree bark; *Chlorella*, in intercellular spaces of Hydra and Planaria.

Order Ulotrichales (Gr. *oulotrios* = woolly-haired) Filament or sheet-like thallus. Cellular differentiation. Beginning of alternation of generations. *Ulothrix*, *Ulua*.

Order Oedogoniales (Gr. *oidein* = to swell + *gonos* = seed) Similar in form and habit to preceding but greater sexual differentiation. Filaments sometimes branched. *Oedogonium*.

Order Conjugales (L. *conjugare* = to unite) Fresh water plants. Single-celled or unbranched filaments. No zoospores or motile cells. Large, conspicuous chloroplasts. *Spirogyra*, desmids.

Order Siphonales (Gr. *siphon* = pipe) Syncytial, tubular, chiefly marine. Produce multinucleate zoospores. Specialized gamete-producing structures. *Vaucheria*.

Order Charales (L. *chara* = a kind of plant) Stoneworts, with lime deposits in stiff, brittle cell walls. Sharply isolated from all other algae. Highly differentiated, as thallophytes. *Chara*, *Nitella*.

CLASS RHODOPHYCEAE (Gr. *rhodon* = rose) Deep-water marine forms, red to purple. More differentiated thallus than previous classes. *Polysiphonia*.

CLASS BACILLARIACEAE (L. *bacillum* = little stick) Diatoms, single-celled or colonial; yellowish brown. Hard, silicious cell walls. Form a large percentage of marine plankton, important as the ultimate food source of many marine vertebrates. *Pinnularia*.

CLASS PHAEOPHYCEAE (Gr. *phaios* = dusky) Largely marine. More highly differentiated than green algae. Reproduction sexual, separate sexes. *Fucus*, *Sargassum*.

Subphylum FUNGI (L. *fungus* = mushroom) The molds, toadstools, yeasts, rusts, blights, and mildews. All lack chlorophyll and are saprophytic or parasitic. Some unicellular, other multicellular and quite complex. Many differ from algae primarily in lack of chlorophyll.

CLASS MYXOMYCETES (Gr. *myxa* = mucus, slime + *mycetos* = fungus) The slime molds. At times syncytial, with peculiar mixture of characteristics of other phyla, sometimes even classed as animals. At times amoeboid, or flagellated, but producing fungoid fruiting bodies. *Fuligo* *varians*.

CLASS PHYCOMYCETES (Gr. *phycos* = seaweed) Molds and mildews. Sometimes called algal fungi but lacking chlorophyll. *Rhizopus nigricans*, *Saprolegnia*.

CLASS ASCOMYCETES (Gr. *askos* = bladder) The blue-green molds, yeasts, with sac-like sporangia or asci. The largest fungus group, about 20,000 species. Plant body of branching hyphae with cross walls. *Penicillium notatum*, *Saccharomyces*.

CLASS BASIDIOMYCETES (Gr. *basis* = base) Rusts, smuts, mushrooms, toadstools. Named for club-shaped spore mother-cells, basidia. The highest of the fungi, probably derived from the Ascomycetes. *Puccinia graminis*, *Agaricus campestris*.

PHYLUM BRYOPHYTA (Gr. *bryon* = moss) Liverworts and mosses (21,000). Aberrant, primitive. Small, moisture-loving. Pronounced alternation of generations, with the sporophyte parasitic on the gametophyte.

CLASS HEPATICAE (Gr. *hepar* = liver) The liverworts; thallus of gametophyte shaped like a liver.

Show how aquatic algae may have become adapted to land life. *Ricciocarpus*, *Marchantia*.

CLASS MUSCI (L. *muscus* = moss) Includes the true mosses. Gametophyte differentiated into stem with simple conducting tissue, leaves, and simple root-like structures. Probably a dead-end offshoot of the Hepaticae. *Funaria*, *Sphagnum*.

PHYLUM PTERIDOPHYTA (Gr. *ptēris* = fern, from *ptēros* = feather) Fern plants and allies (10,000). Advanced vascular plants with marked alternation of generations, but sporophyte is conspicuous and independent phase, while gametophyte is a simple thallus.

CLASS LYCOPODINEAE (Gr. *lykos* = wolf + *pous* = foot) Club mosses and ground pines. Inconspicuous, creeping survivors of a once great group. Transitional reproductive cycle. Gametophytes small and inconspicuous. *Lycopodium*, *Selaginella*.

CLASS EQUISETINEAE (L. *equus* = horse) Horsetails or scouring rushes. Formed like Christmas trees without needles. Inconspicuous scale-like leaves. Straggling survivors of giant ancestors of the Carboniferous. The dioecious gametophyte a simple thallus. *Equisetum arvense*.

CLASS FILICINEAE (L. *filicis* = fern) ¹ The ferns. Recent offshoots of an ancient stock, the most successful survivors of the Pteridophyta. Sporophyte large and independent except in earliest stages. Gametophyte small, inconspicuous thallus. Highly differentiated tissues, complex leaves and vascular stems. Tropical forms attain tree size. *Polystichum*, *Salvinia*.

PHYLUM SPERMATOPHYTA (Gr. *sperma* = seed) The seed plants (150,000). Produce seeds, embryonic sporophytes produced within the tissues of the old. Gametophytes greatly reduced and parasitic within the sporophyte.

Subphylum GYMNOSPERMAE (Gr. *gymnos* = naked, + *sperma* = seed) Fairly primitive seed plants (554). Only four living orders. Large — and small — evergreens. No flowers; seeds not

¹ In a more recently suggested classification, the ferns are not given as a separate phylum, but are included in a greatly expanded phylum, the Tracheophyta or vascular plants, together with the seed plants, as shown below:

PHYLUM TRACHEOPHYTA Vascular plants.

Subphylum LYCOPSIDA Club mosses and ground pines.

Subphylum SPHENOPSIDA Horsetails.

Subphylum PTEROPSIDA Ferns and seed plants.

CLASS FILICINEAE Ferns.

CLASS GYMNOSPERMAE Conifers and related plants.

CLASS ANGIOSPERMAE Plants with enclosed seeds. All higher plants.

enclosed in an ovary, hence the name, "naked seeds."

Order Cycadofilicales (Pteridosperms) The seedferns. Extinct. Existed from the Devonian to the Jurassic. Considered ancestral to the cycads.

Order Cycadales (80) Named after the type species, the Cycad. Traces back to the Triassic. The Mesozoic is sometimes referred to as the age of the cycads. Somewhat like ferns in appearance but have evolved beyond the seed-fern level. *Cycas*.

Order Bennettitales Extinct, common in the Mesozoic. Somewhat like the cycads of today. Flower-like cones. May be ancestors of modern angiosperms.

Order Ginkgoales (1) Single living species, *Ginkgo biloba*, the maidenhair tree of China. Distantly related to cycads but looks like a modern angiosperm.

Order Cordaitales Extinct. Flourished from Devonian through the Carboniferous. Together with seedferns, formed the bulk of the seedplants of the Carboniferous coal forests. They show significant characteristics of seedferns, cycads, and conifers.

Order Coniferales (470) Includes most gymnosperms and most evergreens. Date from the Mesozoic, still successful today. *Pinus strobila*, *Picea alba*, *Thuja occidentalis*.

Order Gnetales (3) Highly specialized. Typical exposed seed. Wood, leaves, and reduced female gametophyte show angiosperm characteristics.

Subphylum ANGIOSPERMAE (Gr. *aggeion* = receptacle + *sperma* = seed) The flowering plants (150,000). Seeds enclosed in an ovary. Most highly evolved plants.

CLASS DICOTYLEDONEAE (Gr. *di* = two + *kotyledon* = cup-shaped hollow, the seed leaf) Includes most flowering plants. Two seed-leaves or cotyledons. Leaves net-veined. Vascular bundles form a cylinder in stem. Flower parts usually in fives, fours, or twos.

Subclass ARCHICHLAMYDEAE Flowers have poorly developed calyx and corolla or these parts not united.

Amentiferae (700). A composite of several orders. Generally wind-pollinated, inconspicuous flowers. Oaks, beeches, chestnuts, hickories, birches, walnuts, alders, and many other trees and shrubs.

Order Ranales (4800) Herbs, shrubs and trees, insect-pollinated; primitive flowers. Often thought to be the oldest dicot order, source of many higher groups. Magnolia, buttercup, columbine, larkspur, laurel, sassafras, camphor, avocado, water lily.

Order Rosales (10,000) A huge order with conspicuous and beautiful flowers. Many of the most important fruit trees; ornamental plants. Flowers generally regular, except in the legumes. Rose, strawberry, blackberry, apple, pear, quince, peach, cherry; legumes, such as bean, pea, clover, peanut, and locust; sedum, stonecrop.

Order Malvales (4000) Herbs, shrubs, and trees, some of considerable economic importance. Cotton, hollyhock, linden, cacao tree, elm, mulberry (silk), breadfruit, fig, hemp.

Order Geraniales (6000) A diversified order related to the Ranales. Geranium, flax, citrus fruits, rubber tree, castor bean, poinsettia.

Order Papaverales (2000) Probably another divergent line evolved from the Ranales. Generally herbs. Poppy, bleeding heart, mustard, cabbages, turnip.

Order Caryophyllales (3500) The pinks. Pinks, beets, spinach, buckwheat, rhubarb.

Order Myrtales (3500) Thought to have evolved from plants resembling the Rosales. Myrtle, eucalyptus, mangrove, evening primrose.

Order Cactales (1200) Generally adapted to desert conditions. The cacti.

Order Celastrales (2000) Vines and woody plants. Bittersweet, grape, Boston ivy, Virginia creeper, mistletoe.

Order Sapindales (1000) Related to the preceding. Horse chestnut, maple.

Order Umbellales (3500) Flowers small in compact flat-topped umbels, as in wild carrot or Queen Anne's lace. Most highly evolved among the Archichlamydeae. Ginseng, English ivy, celery, parsley, parsnip, carrot.

Subclass SYMPETALAE Petals united to form a fused corolla.

Order Ericales (1400) The heaths and allies. Rhododendron, heather, blueberry, cranberry.

Order Ebenales (1000) Related to preceding order. Persimmon. *Achras* (chicle).

Order Primulales (700) Herbaceous. Primrose, cyclamen.

Order Gentianales (2300) Regular five-lobed corollas. Gentian, olive, ash, lilac, forsythia, oleander, milkweed.

Order Tubiflorales (10,000) Conspicuous tubular flowers, generally. Important as food and drug plants. Phlox, morning glory, dodder, potato, tomato, green and red pepper, tobacco, petunia, belladonna, foxglove, spadragon, teak, mint, thyme, lavender, catnip.

Order Rubiales (5000) Trees, shrubs and herbs, flower plan generally in fours. Quinine, coffee, gardenia, honeysuckle, snowberry.

Order Cucurbitales (800) An isolated order of one family. Pumpkin, melons, squashes, cucumber, gourds.

Order Asterales (20,000) Most highly specialized of the dicots; one huge family, the Compositae. Many small flowers form single heads, each like a single flower. Marginal flowers often different from center ones. Daisy, aster, dandelion, goldenrod, marigold, dahlia, zinnia, thistle, burdock, ragweed, sunflower, artichoke, lettuce, wormwood, and a host of others.

CLASS MONOCOTYLEDONEAE Grasses, lilies, and orchids. Embryo has but one cotyledon. Leaves parallel-veined, bundles scattered in the stem. Flower parts in threes or sixes. More recently evolved than the dicots.

Order Alismales (550) Primitive, mostly aquatic or living in swamps. Water plantain, arrowhead, eelgrass, cattail.

Order Glumales (8500) Grasses and sedges. Wind pollinated or self-pollinating. Sedges, bamboo, sugar cane, oats, barley, wheat rye, corn, rice, and nearly all pasture plants.

Order Liliales (5700) Well-developed rootstocks or bulbs. Perennial. Lilies, iris, narcissus, gladiolus, pineapple, banana and allies.

Order Palmales (1200) Exclusively tropical. The palms. Date palm, vegetable ivory, African oil palm, date palm, sago palm.

Order Orchidales (15,000) The single large family of Orchidaceae. The top rung in plant evolution. Worldwide in distribution, some epiphytic and some parasitic. Some remarkably specialized for insect pollination. Famous for beautiful blooms. Lady's slipper, moccasin flower, *Colchicum* — source of the mutation-inducing drug colchicine — ornamental orchids.

Kingdom ANIMALIA (900,000)

Animals are generally easily distinguished from plants by mobility, holozoic nutrition, and weak cell walls. Some Protozoa overlap with the plant kingdom. A few phyla not listed.

PHYLUM PROTOZOA (15,000) (Gr. *protos* = first + *zoon* = animal) Small, many microscopic, single-celled or colonial. Worldwide distribution, usually restricted to water. Four main classes.

CLASS FLAGELLATA (L. *flagellum* = whip) The most primitive Protozoa. Cells bear one or more whip-like structures. The body is given rigidity by a delicate cuticle. Most are free-living, but some are parasitic. *Euglena*, *Pleodorina*, *Volvox*, a large colonial form; *Noctiluca*, *Trypanosoma gambiense*.

CLASS RHIZOPODA (Gr. *rhiza* = root + *pous* = foot) Characterized by root-like "false feet" or pseudopods. Protoplasm delimited by a delicate cell membrane. Some form external shells or internal stiffening skeletons. Among them, the Foraminifera have snail-like shells, the Heliozoa often produce sun-like internal skeletons, and the Radiolaria produce similar skeletons from within a frothy gelatinous mass. Some tend to form colonies. Most are free-living, some parasitic. *Amoeba proteus*; *Endamoeba histolytica*, *Globigerina*, a foraminiferan, *Lychnosphaera*, a radiolarian.

CLASS SPOROZOA (Gr. *sporos* = sowing) Parasitic, usually without locomotor structures or ingestive organs. Reproduction by multiple fission or sporulation. *Plasmodium vivax*, *Nosema bombycis*, *Babesia*.

CLASS CILIATA (L. *cilium* = eyelid, eyelash) Protozoa having hair-like appendages, cilia. Highly varied in form and habit and found in all waters the world over. Some single, some colonial; most are highly active. Four orders, according to the arrangement of cilia: *holotrichs*, with cilia uniformly covering the body; *heterotrichs*, with cilia enlarged and cemented to form membranelles; *hypotrichs*, with few cilia hypertrophied as leg-like bristles. Suctorians, adults having no cilia, but have tentacular tubes with which they suck other protozoans dry. *Paramoecium*, a holotrich; *Stentor*, a heterotrych; *Stylonychia*, a hypotrich; *Podophyra*, a suctorian.

PHYLUM PORIFERA (L. *porus* = pore + *ferre* = to bear) The sponges (15,000). The most primitive metazoans, once thought colonial flagellates. Inert, fleshy lumps usually in the ocean, but small forms are also found in fresh water. Many small openings lead into canals through which water is circulated for feeding and breathing.

CLASS CALCAREA (L. *calcaris* = limy) Skeleton of limy spicules. *Leucosolenia*, *Grantia*.

CLASS HEXACTINELLIDA (Gr. *hex* = six + *aktinos* = ray — of light) Skeleton of siliceous spicules having three axes, hence six rays. Deep-sea glass sponges. *Euplectella*, Venus' Flower Basket.

CLASS DEMOSPONGIAE (Gr. *demos* = the people, *spongia* = sponge) Probably evolved from siliceous sponges. Some have siliceous spicules, but not triaxial, other have a spongin skeleton. The latter used as bath sponges. *Euspongia*, the sponge of commerce; *Spongilla*, a fresh water form.

PHYLUM COELENTERATA (9,000) (Gr. *kóilos* = hollow + *enteron* = intestine) The first "true" metazoans. Probably evolved from different protozoan ancestors than the sponges. From coelenterates most higher animal phyla probably

came. Basic plan a sac with two layers of cells. Central mouth surrounded by tentacles. Sea anemones, the coral polyps, jellyfishes. Most are marine, though some found in fresh water.

CLASS HYDROZOA (Gr. *hydra* + *zoön* = animal) Small individual polyps, some colonial. Usually an alternation of generations, polyp phase dominant. *Hydra*, *Obelia*, *Physalia*, the Portuguese man-o'-war.

CLASS SCYPHOZOA (Gr. *skypnos* = cup) Main phase is medusa. Polyps, where produced, are small and degenerate. The common jellyfishes. *Aurelia*, *Chrysaora*.

CLASS ANTHOZOA (Gr. *anthos* = flower) No alternation of generations. Sea anemones and coral polyps. Polyp phase only. *Corallium nobile*, the precious coral; *Metridium*, the common pinkish sea anemone.

PHYLUM CTENOPHORA (100) (Gr. *kteis* = comb) The comb jellies. Transparent jelly-like bodies have eight rows of fused, comb-like cilia. Outward symmetry radial, inward bilateral. Some have third tissue layer, mesoderm. Some bottom-living forms are flattened and resemble higher Platyhelminthes. *Cestus*, Venus' Girdle; *Coeloplana*, a flattened bottom-living form.

PHYLUM PLATYHELMINTHES (7000) (Gr. *platys* = flat + *helminthes* = worm) The flatworms. Three cell layers. Logical continuation of coelenterate and ctenophore lines. General organization primitive, but increased absorptive area in digestive tract, more centralized nervous system, and excretory system. Hence greater size and increased activity.

CLASS TURBELLARIA (L. *turba* = disturbance) Free-living, soft-bodied "worms," living in fresh or salt water, and sometimes on land. Cilia around edges and on the lower surface provide locomotion. A few are parasitic. *Planaria*.

CLASS TREMATODA (Gr. *trematodes* = having pores) Flukes. Parasites. Many have multiple suckers or pores. *Fasciola*, the sheep liver fluke.

CLASS CESTODA (Gr. *kestos* = girdle) The tapeworms. Parasitic, highly adapted.

PHYLUM NEMERTINEA (Gr. *nemertes* = unerring) Proboscis worms. Uncertain relationship, sometimes classed as flatworms. Uniform ciliary covering, diffuse third tissue layer, excretory flame cells. First show tubular digestive system from mouth to anus, and blood-vascular system. Larva similar to the trochophore larva of higher phyla and to the adults of the trochelminthes.

PHYLUM NEMATHELMINTHES (3000) (Gr. *nema* = thread) Roundworms or threadworms. Extremely numerous, both free-living and para-

sitic, some on man. Tough outer cuticle permits bending motions. Spindle-shaped, 1 mm. to 10 cm. long. Tubular digestive and excretory tract. *Necator americanus*, the hookworm; *Trichina spiralis*, *Ascaris*, intestinal parasites.

PHYLUM TROCHELMINTHES (1800) (Gr. *trochos* = wheel) The rotifers. Ring of beating cilia around mouth looks like a revolving wheel. Smaller than many protozoans, but surprisingly complex. Tubular digestive tract divided into organs, well-developed central nervous system, excretory flame cells, well-organized muscular system. Certain species show marked structural resemblance to larval forms of other phyla, such as annelids and mollusks. *Trochosphaera*, *Melicerita ringens*.

PHYLUM BRACHIOPODA (130) (Gr. *brachion* = arm + *podos* = foot) The lampshells. Of ancient lineage -- the Cambrian -- and uncertain relationship. A few living forms almost identical with those of several hundred million years ago. Superficially like mollusks. Larva resembles the trochophore. *Lingula*.

PHYLUM BRYOZOA (3000) (Gr. *bryon* = moss + *zoön* = animal) Uncertain classification. Superficial resemblance to coelenterates. Tubular body with crown of ciliated tentacles. Usually in colonies like a coat of moss. Somewhat like brachiopods in structure. Fresh water. *Plumatella*.

PHYLUM ANNELIDA (7000) (L. *annulus* = little ring) The segmented worms, the first organisms that distinctly belong to the higher metazoans. Segmental body plan, tubular differentiated digestive tract, body cavity or coelom, centralized nervous system (ventral), kidneys or nephridia, blood-vascular circulation. Distinct head end and bilateral symmetry. World-wide distribution.

CLASS ARCHIANNELIDA (Gr. *archi* = first) Primitive or degenerate. Lacking bristle-like appendages of the following class to which they are most closely related. *Polygordius*.

CLASS CHAETPODA (Gr. *chaite* = hair) Bristle-like appendages, typically segmented but varying greatly in appearance.

Subclass OLIGOCHAETES (Gr. *oligos* = small, few, scant) Having few bristles. *Lumbricus*, *Tubifex*.

Subclass POLYCHAETES (Gr. *polys* = many) Many bristles. Largely marine. *Nereis*; *Aphrodite*, the sea mouse.

CLASS HIRUDINEA (L. *hirudo* = leech) The leeches. Without bristles, but segmented. Anterior and posterior suckers. *Hirudo medicinalis*.

CLASS GEPHYREA (Gr. *gephyra* = bridge) Once thought to be a bridge between annelids and echinoderms. Degenerate; trochophore-like larva

first develops into a segmented worm with a coelom. Later segmentation and coelom disappear. Sac-like. Live in burrows on ocean bottom. *Bonellia viridis*.

PHYLUM MOLLUSCA (80,000) (L. *molluscus* = soft) Highly specialized and successful invertebrates. Remotely connected with those more conservative creatures that led to the arthropods. Body soft and unsegmented, frequently with hard outer shell.

CLASS AMPHINEURA (Gr. *amphi* = double, on both sides + *neuron* = nerve) Primitive centralized nervous system in two lateral strands. Shell articulated. *Chiton*.

CLASS GASTROPODA (Gr. *gaster* = belly + *podos* = foot) Walk on the "belly" which has become a foot. Body coiled or straight. Many have shells. The snails and slugs. *Lymnaea*, a freshwater snail; *Helix pomatia*, the edible snail.

CLASS SCAPHOPODA (Gr. *skaphe* = boat) Elephant's tusk shells. Long furrows in the digging foot. Sand-diggers. *Dentalium*.

CLASS PELECYPODA (Gr. *pelekos* = hatchet) Hatchet-shaped foot. The mussels, clams, oysters, scallops, and shipworms. A sharply distinct class, characterized by two-piece hinged shell. Hence "bivalves." Burrow in mud or sand, or attach to solid objects by adhesive threads. *Anodonta*, fresh water mussel; *Ostrea*, the oyster; *Pecten*, the scallop.

CLASS CEPHALOPODA (Gr. *kephale* = head) The "head-feet," nautiloids, squids, and octopods. Perhaps the weirdest of all large animals, and the largest invertebrates. They are strictly marine. High brain development. Body encased in a fleshy mantle. Two subclasses, *Protocephalopoda*, including the *Nautiloidea* and the extinct *Ammonoidea*; and *Melacephalopoda*, the *Octopoda* and the *Decapoda*, octopods and squids. *Nautilus*; *Octopus*; *Loligo*, the squid.

PHYLUM ARTHROPODA (700,000) (Gr. *arthron* = joint) A vast phylum, the culmination of invertebrate evolution. Includes insects. Many-jointed appendages. Exoskeleton. Segmented body, like the annelids. Ventral nervous system connected to dorsal cerebral ganglion. Bilateral symmetry. Respiration by gills or tracheae. Usually a heart and a circulatory system. In lower arthropods, excretion by segmental nephridia; in others by special organs, unrelated to nephridia. Segments variously specialized for different functions.

CLASS ONYCHOPHORA¹ (Gr. *onychos* = claw) Segmented; looking a little like a caterpillar. Some-

what uncertain classification. Combine characteristics of annelids and arthropods. Not an actual link between these phyla, but the type of organism that might have been. *Peripatus*.

CLASS TRILOBITA (Gr. *tri* = three + *lobos* = lobe) Extinct. Probably a general stem form of arthropod. Three-lobed body plan.

CLASS CHILOPODA (Gr. *cheilos* = combining form meaning lip) The centipedes. The jaw-like, often poisonous fangs are modified feet. Serpentine body of many similar, flattened segments, each with a pair of legs. Voracious and predatory. *Scolopendra*, a tropical centipede.

CLASS DIPLOPODA (Gr. *diplos* = double) Popularly misnamed millipedes or "thousand leggers," they may have several hundred legs. Body is cylindrical, of many similar segments, each with two pairs of legs. Vegetarian. *Iulus terrestris*, the common millipede.

CLASS CRUSTACEA (L. *crusta* = crust) The crabs, lobsters, and shrimps. Hard exoskeleton, often stiffened with lime deposits. Body usually in three parts, head, thorax, abdomen. In higher forms head and thorax fuse. Appendages frequently highly modified but all with same basic plan. Most are aquatic and breathe by gills. Many have nauplius larva.

Subclass COPEPODA (Gr. *kope* = oar) Simple and primitive. Relatively little difference between segments. Appendages still show common origin. *Cyclops*, a common freshwater form.

Subclass BRANCHIOPODA (Gr. *branchia* = gills) Remarkable continuity of form from species to species but considerable divergence between the two ends of the series. Some have many segments; some few, hidden by external body flaps or shields. Most are freshwater forms, unlike most other crustaceans. *Daphnia pulex*, the water flea.

Subclass OSTRACODA (Gr. *ostrakon* = tile, shell) Minute. Body enclosed in clam-like shells. *Cypripina mediterranea*.

Subclass CIRRIPIEDIA (L. *cirrus* = curl, ringlet) Barnacles. Sessile crustaceans. *Balanus*, the common barnacle; *Lepas*, the goose barnacle; *Sacculina*, parasite of other crustaceans.

Subclass MALACOSTRACA (Gr. *malakos* = soft + *ostrakon* = shell) Includes the largest and best known crustaceans.

Order Amphipoda (Gr. *amphi* = double) A fairly large order of marine crustaceans, though some are freshwater forms. Laterally flattened, shrimp-like; uniform segmentation. *Gammarus*, a genus containing fresh- and saltwater forms.

Order Isopoda (Gr. *isos* = equal) Fresh- and saltwater forms, and some adapted to land life. *Oniscus asellus*, the sowbug.

¹ Sometimes classified as a separate phylum.

Order Decapoda (Gr. *deka* = ten) Far the largest group of crustaceans (8000). Anterior thirteen segments fused into cephalothorax, of which eight form the thorax. *Homarus*, lobster; *Cambarus*, crayfish; *Palaemonetes*, shrimp.

CLASS ARACHNOIDEA (Gr. *arachne* = spider) Widely differentiated forms. Body divided into cephalothorax and abdomen. Four pairs of walking legs attached to the cephalothorax. No antennae. Spiders, scorpions, ticks, and mites.

Subclass XIPHOSURA (Gr. *xiphos* = sword + *oura* = tail) But one genus, *Limulus*, the horseshoe crab, unchanged since the Triassic, and suggesting the aquatic ancestors of modern terrestrial arachnoids.

Subclass ARACHNIDA All arachnoids but *Limulus*.

Order Scorpionida The scorpions. Elongated abdomen has terminal poison claw. Pair of head-appendages with pincers. *Centurus*, scorpion of tropical America.

Order Phalangida The daddy long-legs.

Order Araneae The spiders A large group (20,000), remarkably uniform. Large unsegmented abdomen. Four pairs of legs, and one pair of leg-like head appendages, pedipalps (tactile organs). Jaws often equipped with poison glands. Usually four pairs of eyes. Spinnerets in abdomen produce web. Respiration by book lungs. *Lycosa helluo*, the wolf spider; *Latrodectus mactans*, the black widow spider.

Order Acarina The mites and ticks. Degenerate and largely parasitic. No external evidence of metamerism. *Trombicula autumnalis*, the chigger of the South; *Boophilus annulatus*, Texas cattle tick; *Sarcoptes scabiei*, causes scabies.

CLASS INSECTA Probably nearly a million species. Body in three sections, head (usually six segments), thorax (usually three), and abdomen (eleven or less). Mainly adapted to land life, insects also live in water, and many have aquatic larval stages. Seventeen prominent orders of the two dozen known are here listed.

Order Protura (Gr. *protos* = first) Little known, tiny, and primitive. Besides thoracic legs, three pairs of leg-like abdominal appendages, a primitive condition unique among insects. Segments all similar. No real metamorphosis, no wings, compound eyes, or antennae. *Acerentomon doderoi*.

Order Thysanura (Gr. *thysanos* = tassel + *oura* = tail) Primitive, wingless. Chewing mouthparts, little differentiation of segments. No real metamorphosis. *Lepisma saccharina*, the silverfish.

Order Collembola (Gr. *colla* = glue + *embolon* = wedge) The "springtails." Exude a glue-like

material with which they fasten themselves to their substrate. Primitive, wingless, generally with chewing mouthparts. No real metamorphosis. *Entomobrya laguna*.

Order Orthoptera (Gr. *orthos* = straight + *pteron* = wing) Grasshoppers, leafhoppers, crickets, cockroaches, and many others. Forewings generally leathery, hindwings pleated. Chewing mouthparts. Metamorphosis incomplete. Except praying mantis, most are vegetarian. *Brachystola magna*, lubber grasshopper; *Stagomantis carolina*, praying mantis; *Gryllus campestris*, cricket; *Blatta orientalis*, cockroach.

Order Isoptera (Gr. *isos* = equal) The termites or white ants. Primitive but with highly organized social structure. Both pairs of wings similar. Chewing mouthparts. Metamorphosis incomplete. Ability to digest wood attributed to the presence of symbiotic Protozoa in their intestinal tract. *Termes*, termite.

Order Neuroptera (Gr. *neuron* = nerve) The lace-winged flies, with four membranous, iridescent wings. Mouthparts equipped for chewing. Metamorphosis complete. *Corydalus cornutus* (the larval form) the hellgramite, used as bait for fishing.

Order Ephemera (Gr. *ephemeros* = lasting but a day) Lacy wings, rear wings smaller than front ones or lacking. Mouthparts of adults vestigial; they do not eat. Aquatic larvae may live for years. *Ephemera simulans*, mayfly.

Order Odonata (Gr. *odous* = a tooth) Dragon and damselflies. Chewing mouthparts. Many are brilliantly colored, and they are strong fliers. The nymph (larva) is an aquatic predator. Earliest true dragonflies date from the Permian. *Aeschna grandis*, a dragonfly; *Calopteryx*, damselfly.

Order Anoplura (Gr. *anoplos* = unarmed) True lice (distinct from book lice and bird lice). Wingless, parasitic. Piercing and sucking mouthparts. No metamorphosis. Eyes degenerate. *Pediculus humanus capitis*, the head louse; *P. humanus corporis*, the body louse.

Order Hemiptera (Gr. *hemi* = half) Front wings leathery over the basal half; membranous ends overlap on the back, suggesting half wings. The true bugs. Generally flattened and blunt. Piercing and sucking mouthparts. Metamorphosis incomplete. Though some are predaceous, most are harmful garden pests. *Pentatomidae*, stinkbugs; *Blissus leucopterus*, the chinch bug; *Cimex lectularius*, the bedbug; *Belostoma indicum*, an aquatic hemipteran of India, measuring over three inches.

Order Homoptera (Gr. *homos* = same) Variable; most have four similar wings, others have

hind wings reduced or absent. Mouthparts for piercing and sucking. Metamorphosis generally incomplete. *Erythroneura zizac*, grape leafhopper; *Aspidiotus perniciosus*, San Jose scale; *Aphis roseus*, the rosy apple aphid; *Tibicina septemdecim*, the seventeen-year "locust."

Order Coleoptera (Gr. *coleos* = sheath) Chitinous front wings form a shield over the membranous hind ones. The beetles, the largest insect order, over 200,000 species! Chewing mouthparts, complete metamorphosis. Some are excellent fliers, others do not fly. Some gigantic, for insects. *Lepidoptera decemlineata*, the Japanese beetle; *Phyllorhaga*, the Junebug; *Macrodactylus subspinosus*, the rosebug; *Phyllotreta vitata*, the flea-beetle; *Anthonomus grandis*, the cotton-boll weevil.

Order Trichoptera (Gr. *trichos* = hair) Wings covered with silky hairs. Moth-like insects with aquatic larvae, the caddice flies. *Hydropsyche partita*.

Order Lepidoptera (Gr. *lepido* = scale) The moths and butterflies. Tiny scales cover the wings and give them a velvety appearance. Generally four wings. Mouthparts generally for sucking, though degenerated in some. Larvae are caterpillars (L. *catta pilosa* = hairy cat); complete metamorphosis. *Tineola biselliella*, the clothes-moth; *Galleri mellonella*, the wax-moth; *Porthetria dispar*, the gypsy moth; *Euproctis chrysorrhoea*, the brown-tail moth; *Malacosoma americana*, the tent-caterpillar; *Carpocapsa pomonella*, the codling moth; *Pyrausta nubilalis*, the European corn-borer; *Bombyx mori*, the silkworm.

Order Diptera (Gr. *dis* = twice) Front wings only. The flies, mosquitoes, and midges. Sucking mouthparts. Metamorphosis complete. *Culex*, the common mosquito; *Aedes*, the yellow-fever mosquito; *Anopheles*, the malaria mosquito; *Musca domestica*, the housefly.

Order Siphonaptera (Gr. *siphon* = a tube + *aptera* = without wings) The fleas, with siphon-like sucking tube and no wings. Metamorphosis is complete. May carry diseases, such as bubonic plague. *Pulex irritans*, the human flea; *Ctenocephalus felis*, the cat flea; *Ctenocephalus canis*, the dog flea.

Order Hymenoptera (Gr. *hymen* = membrane) The bees, wasps, and ants, with membranous wings. Mouthparts chewing, sucking, or both. Females generally have stings. Metamorphosis complete. The most highly developed social life of all creatures. The ants are the dominant family.

PHYLUM ECHINODERMATA (5000) (Gr. *echinos* = hedgehog + *derma* = skin) Starfishes, sea-urchins, and sea-cucumbers. Body-cavity or coelom, unusual body-forms. Rather highly

evolved animals, leading to the Chordata. Primarily radial symmetry, usually in fives. Organ systems extend into all arms. Central mouth on ventral surface. Locomotion by tubular feet.

CLASS ASTEROIDEA (Gr. *aster* = star + *eidos* = form) The common starfishes. Arms not marked off sharply from body. Usually five arms, sometimes more. *Asterias*.

CLASS OPHIUROIDEA (Gr. *ophis* = serpent + *oura* = tail) Brittle stars. Experts at self dismemberment under stress. Sinuous arms may be repeatedly forked, as in the basket stars. Arms sharply marked off from disc-like body. *Ophiocreas oedipus*.

CLASS ECHINOIDEA (Gr. *echinos* = hedgehog + *eidos* = form) Sea-urchins, looking somewhat like spiked pincushions. Movable spines may be used for walking. No arms; box-like skeleton. *Arbacia*, common sea-urchin; *Echinarachnius parma*, the sand-dollar.

CLASS HOLOTHUROIDEA (L. *holothuria* = "a sort of water polyp") Sea cucumbers. Pliable and leathery body; no spines. Differ from other echinoderms in lying on their sides, thus having secondary bilateral symmetry. *Cucumaria planici*; *Pentacta frondosa*.

CLASS CRINOIDEA (Gr. *crinon* = lily) Sea lilies. Stalked, like flowers. Some break from stalks and become free-living. Arms may be branched and have lateral processes. *Pentacrinus*; *Rhizocrinus*.

PHYLUM CHORDATA (36,000) (L. *chorda* = cord) Segmental structure; dorsal notochord; tubular dorsal nervous system; tubular ventral alimentary canal; segmental pharyngeal gills or gill clefts.

Subphylum HEMICHORDA (Gr. *hemi* = half + *chorda*) Obscure, wormlike, marine. Notochord-like structure in front part of body. *Balanoglossus*, the acorn-tongue-worm.

Subphylum UROCHORDA (Gr. *oura* = tail + *chorda*) Tunicates or sea-squirts. Degenerate, sessile marine creatures, lacking most chordate characteristics in the adult form. Larva shows typical chordate features. *Pyura aurantium*.

Subphylum CEPHALOCHORDA (Gr. *kephale* = head + *chorda*) Small, translucent fish-like. No distinct head. Notochord and neural tube extend most of the length of body at all stages. Clearly displays the general chordate features. *Amphioxus*.

Subphylum VERTEBRATA (L. *vertebratus* = jointed) Backboned animals (most chordates). Embryonic notochord generally replaced by vertebral column, part of endoskeleton, in lower verte-

brates of cartilage and in higher ones of bone. Generally a tail. Head usually distinct. Usually two pairs of appendages. Ventral heart with two to four chambers; blood has red cells carrying hemoglobin. Anterior portion of nervous system is expanded into a brain. Large coelom houses internal organs.

CLASS CYCLOSTOMATA (Gr. *cyclos* = round + *stoma* = mouth) Most primitive and degenerate vertebrates. Eel-like, jawless, limbless.

Subclass MYXINOIDEA (Gr. *myxinos* = slimefish) Hagfishes, the lowest living vertebrates. Secrete quantities of slime. Four pairs of tentacles surround a small mouth. Vestigial eyes, separate openings for intestinal and urinary tract and sexual ducts. Hermaphroditic, no metamorphosis.

Subclass PETROMYZONTIA (Gr. *petra* = stone + *myzontos* = sucked in) Lampreys. About three feet long. Inhabit both fresh and salt water. Large round, sucker-like buccal funnel studded with chitinous teeth. Margin of funnel supported by annular cartilage. Real mouth lies at its bottom. Seven pairs of gill slits open separately to outside. Poorly developed eyes. Single dorsal nostril. Predatory or semiparasitic.

CLASS CHONDRICHTHYES (Gr. *chondros* = cartilage + *ichthys* = fish) Cartilaginous fish, sharks, skates, and rays. Paired fins, paired jaws, fish-like gills and gill-arches. Gills have separate openings. No swim bladder. The body is covered with tooth-like placoid scales. A rudimentary notochord persists.

Subclass ELASMOBRANCHII (Gr. *elasmos* = metal plate + *branchia* = gill) Includes most cartilaginous fishes.

Order Selachii The sharks. *Squalus*.

Order Batoidea Skates and rays. Peculiarly flattened, bottom-living creatures, rather square in outline, with the mouth end at one corner and the tail at the opposite one. Butterfly ray.

Subclass HOLOCEPHALI (Gr. *holos* = whole + *kephale* = head) Chimaeras or rat-fishes, rare, odd and obscure.

CLASS OSTEICHTHYES (Gr. *osteon* = bone + *ichthys*) The bony fishes, the bulk of all fresh water as well as marine fishes. Skeleton is largely of bone. Gills are covered by a single bone-supported flap on each side. Scales usually present but are never placoid. Two sets of paired fins. Most have a swim bladder.

Order Chondrostei (Gr. *chondros* = cartilage + *osteon* = bone) Primitive ray-finned fishes with skeletons still mainly cartilaginous. With the *Holostei*, are often referred to as Ganoids (Gr. *ganos* = brightness) from their shiny ganoid

scales. *Acipenser*, sturgeon; *Polypterus*, African bichir, the most primitive of ray-finned fishes.

Order Holostei (Gr. *holos* = whole + *osteon* = bone) Similar to the Chondrostei, but with bony skeletons. *Lepidosteus*, garpike; *Amia*, bowfin.

Order Teleostei (Gr. *teleos* = complete) The "true" bony fishes, probably descended from ganoid types. The bulk of all fishes. Most advanced and most recent. Scales are thin and transparent rather than enameled as in previous orders. A bewildering variety of adaptive forms. *Clupea*, herring; *Prionotus*, sea robin; *Scomber*, mackerel.

Order Crossopterygii (Gr. *crossoi* = fringe + *pterygion* = little fin) An ancient stock, the "lobe-finned fishes," from which sprang the land vertebrates. Long thought to be extinct.

Order Dipnoi (Gr. *dis* = twice + *pnoe* = breath) An ancient stock, related to, but early separated from the crossopterygians. The lungfishes of today, African, South American, and Australian.

CLASS AMPHIBIA (Gr. *amphibios* = leading a double life) Generally aquatic larva. Skin generally soft, moist, and glandular. Most have four appendages with digits. Eyes usually have lids.

Order Urodela (Gr. *oura* = tail + *delos* = visible) Tailed amphibians, usually with fore and hind limbs similar in size. The salamanders and newts. *Ambystoma tigrinum*.

Order Salientia (L. *salientis* = leaping) Also called Anura (Gr. *an* = not + *ouros* = tail). Frogs and toads. Tailless amphibians with powerful hind legs and small front legs. Bull frog (*Rana catesbeiana*).

Order Apoda (without feet) Limbless, worm-like; imbedded degenerate scales. Tropical animals not closely related to other amphibians. Often referred to as cecilians or blindworms. *Ichthyophis glutinosa*.

CLASS REPTILIA (L. *repere* = to creep) Highly divergent in form. Body generally divided into head, trunk, and tail. Generally four limbs, though these may be absent (snakes). Most have dry scaly skins. Except in snakes, eyes have movable lids. Eggs are large and leathery. No larval stage. In some, the heart has two almost separate ventricles.

Order Rhynchocephalia (Gr. *rhynchos* = snout + *kephale* = head) Contains but a single living genus, the primitive tuatara (*Sphenodon punctatum*) of New Zealand.

Order Crocodilia (Gr. *krokodeilos* = crocodile) The crocodiles, alligators, caymans, and gavials. Large reptiles, up to 30 feet long, distributed throughout the tropical world. The only surviving archosaurs. *Alligator mississippiensis*; *Caiman*

latirostris, of the Amazon; *Gavialis gangeticus*, of India; *Crocodylus americanus*.

Order Testudinata (L. *testudinatus* = like a tortoise) The turtles and tortoises. Vertebrae, ribs, and dermal bones fused to form bony box with horny scales. *Chrysemis picta*, the painted turtle; *Chelydra serpentina*, the snapping turtle.

Order Squamata (L. *squamatus* = scaly) The lizards and snakes.

Suborder **Lacertilia** (L. *lacertus* = lizard) The lizards. The most "typical" of reptiles because least specialized. But a few are legless, while others fly or glide. *Tarentola mauritanica*, the wall gecko; *Draco volans*, the flying dragon.

Suborder **Ophidia** (Gr. *ophis* = snake) Slender and limbless except for rudimentary hind legs in some pythons. Lidless eyes. Some have highly specialized poison mechanisms. *Crotalus horridus*, the timber rattler; *Tropidonotus*, the garter snake; *Lachesis lanceolata*, the fer-de-lance.

CLASS AVES (L. *avis* = bird) Warm blooded, feathered, winged vertebrates. Living birds have no teeth, but horny bills. Reproduction by hard-shelled eggs. Two ventricles of heart are separate, thus introducing the double closed circulatory system.

Subclass **ARCHAEORNITHES** (Gr. *archaios* = ancient + *ornithes* = bird) The fossil *Archaeopteryx*. Tail still long and bony; teeth.

Subclass **NEORNITHES** (Gr. *neos* = new) The modern birds.

Division Ratitae (L. *ratis* = raft) With flat breastbone, rudimentary wings. Ostrich, kiwi, cassowary, emu. Four orders.

Division Carinatae (L. *carina* = a keel) The winged birds. Keeled sternum for attachment of flight muscles. Includes most modern birds.

Order Tinamiformes The Tinamu. Partridge-like, weak fliers of South America. Related to the Ratitae, but the breastbone is keeled.

Order Sphenisciformes (Gr. *spheniskos* = little wedge) The penguins. Small, scale-like feathers.

Order Gaviiformes (*Gavia* = the loon) Loons, excellent swimmers and divers.

Order Colymbiformes (Gr. *kolymbos* = diver) The grebes. Rudimentary tail, lobed toes. Excellent swimmers and divers.

Order Procellariiformes (*Procellaria*, the stormy petrel) Marine fliers. Webbed feet. Wing span up to 10 feet. Rarely come to land except to breed. Albatross, petrel.

Order Pelecaniformes (L. *pelicanus* = pelican) Swimming birds. Webbed toes. Pouched beak. Pelicans, cormorants.

Order Ciconiiformes (L. *ciconia* = stork) Stork-like, long-legged, javelin-beaked, wading birds. Heron, ibis, flamingo.

Order Anseriformes (L. *anser* = goose) Broad sensitive bill. Webbed feet. Geese, ducks, swans.

Order Falconiformes (L. *falcon* = falcon) Birds of prey. Hooked bills. Hawks, eagles, vultures.

Order Galliformes (L. *gallus* = a cock) Terrestrial birds. Pheasants, quail, turkey, domestic fowl.

Order Gruiformes (L. *grus* = crane) Crane-like birds, mostly waders. Partially webbed feet. Crane, rail.

Order Charadriiformes (*Charadrius*, a genus of plover) Small shore-birds, long-legged and long-billed. Plover, gull, tern, sandpiper, snipe.

Order Columbiformes (L. *columba* = pigeon) Short bills and wings. Pigeons, doves.

Order Psittaciformes (L. *psittacus* = parrot) The parrots. Four toes in opposed pairs, heavy hooked bills.

Order Cuculiformes (L. *cuculus* = cuckoo) Cuckoos and similar types. Four toes, in opposite pairs, for perching. Some are nest parasites.

Order Strigiformes (L. *strix* = screech owl) Owl-like birds. Nocturnal, predatory. Large eyes. Silent flight.

Order Caprimulgiformes (lit., "goat-milker," from *caprimulgus*, generic name of European goat-sucker) None of them "suck goats." Birds with wide mouths, for catching insects on the wing. Long pointed wings. Nighthawk, whip-poor-will.

Order Micropodiformes (Gr. *mikros* = small) Small feet. Expert fliers. Swifts, hummingbirds.

Order Coraciiformes (Gr. *corax* = crow) Kingfisherlike birds, not crows. Long, usually straight bills, small legs. Kingfisher, hornbill.

Order Piciformes (L. *picus* = woodpecker) A brace-like tail for climbing. Heavy boring bill. Protrusible barbed tongue in woodpecker. Woodpecker, toucan.

Order Passeriformes (L. *passer* = sparrow) By far the largest order of birds, including fully half the known species. Sparrows, tanagers, blackbirds, nuthatch, finches, wrens, vireos, starlings, robins, thrushes, crows, larks, swallows.

CLASS MAMMALIA (3000 species) (L. *mamma* = breast) The most diverse and adaptive vertebrates, most capable in learning and reasoning. Warm-blooded, covered with hair. Viviparous; young fed with milk produced in special glands. Double circulatory system as in birds. 18 orders.

Subclass **PROTOTHERIA** (Gr. *protos* = first + *therion* = animal) One order, the Monotremata,

with combined urogenital and intestinal opening through cloaca. *Ornithorhynchus anatinus*, the duckbilled platypus.

Subclass METATHERIA (Gr. *meta* = between) The pouched mammals. One order, Marsupialia (L. *marsupium* = pouch). Characteristic mammals of Australia; few elsewhere. *Macropus*, a kangaroo; *Didelphis*, the opossum.

Subclass EUTHERIA (Gr. *eu* = well, good) The "proper" or "real" mammals, also called placental. All well-known mammals.

Order Insectivora (L. *vorare* = to devour) Insect eaters. Small, generally primitive. Sharp needle-like teeth, poor brain development. Many features of early mammalian ancestors. *Talpidae*, the moles; *Tupaia*, the tree shrew; *Erinaceus*, the European hedgehog.

Order Chiroptera (Gr. *cheir* = hand + *pteron* = wing) The bats, the only mammals capable of true flight. Two suborders, the fruit eaters and the insect eaters. *Pteropus*, the fruit-eating bat or "flying fox"; *Myotis*, the common bat.

Order Edentata (L. *e* = without + *dens* = tooth) Odd, highly specialized. Most have reduced teeth; some, like the giant anteater, have none. *Tatus*, the Armadillo; *Myrmecophaga*, the giant anteater.

Order Pholidota (Gr. *pholis* = scale + *osis* = state) African and Asiatic scaly anteaters, covered with horny scales, except hairy ventral surface. *Manis temmincki*, of East Africa.

Order Rodentia (L. *rodere* = to gnaw) The gnawers: rats, mice, gophers, woodchucks, squirrels, and scores of others. In numbers, the largest and most successful mammalian order. *Epimys rattus*, the Norwegian rat.

Order Lagomorpha (Gr. *lagor* = hare + *morphe* = form) Rabbits and hares.

Order Carnivora (L. *carnis* = flesh + *vorare* = to devour) Most flesh-eating mammals, some omnivores, such as bears. Well-developed canines, small incisors, shearing molars. Lions, cats, dogs, bears, seals, and walrus (Pinnipedia).

Order Artiodactyla (Gr. *artios* = even + *daktylos* = toe or finger) Even-toed ungulates. The ruminants, cattle, goats, and sheep. Also such non-ruminants as the pig.

Order Perissodactyla (Gr. *perissos* = odd) The odd-toed hoofed animals. Rhinoceros (three toes), tapir (four on the front, three on the hind feet), horse (one toe).

Order Proboscidea (Gr. *pro* = before + *boscein* = to feed) The elephant, the largest modern land animal.

Order Sirenia (Gr. *siren* = a sea nymph) The sea cows, dull herbivores little resembling their relatives the proboscideans. The dugong; *Trichechus latirostris*, the Manatee.

Order Cetacea (L. *cetus* = whale) Some are the largest animals of all time. Often given as two orders, the *Odontoceti*, toothed whales; the *Mystacoceti*, whalebone whales. *Balaenoptera*, the blue whale; *Delphinus*, dolphin.

Order Primates (L. *primatus* = first) The lemurs, monkeys, apes, and man. Most highly developed cerebral cortex, but some primitive features.

Suborder Lemuroidea (L. *lemures* = ghost, specter) Long snout, long bushy tail, inferior intelligence. Nocturnal in habit. Most abundant on the island of Madagascar.

Suborder Tarsiodea (Gr. *tarsos* = flat footed) One living species, *Tarsius*. Superior to lemurs, inferior to monkeys. Round head, short snout, immense eyes on a swiveling head. Long hind legs, toes with vacuum disks. Insectivorous, nocturnal, arboreal. Thought close to the line of man.

Suborder Anthropeidea (Gr. *anthropos* = man) All other primates. Two main groups, *Platyrrhini* (Gr. *platys* = broad, flat + *rhis* = nose), New World monkeys; and *Catarrhini* (Gr. *kata* = down), including the Old World monkeys. The four families of the Catarrhini are:

Family Cercopithecidae (Gr. *kerkos* = tail + *pithecos* = ape) All the Old World monkeys, the baboons, mandrill, macaque, rhesus, mangabey, colobus, and many others.

Family Hylobatidae (Gr. *hylobates* = one that walks in the woods) The gibbons, small apes restricted to the Malay peninsula. Enormously long arms. Can walk readily on its legs without use of its arms. Except for arms, body proportions close to man's but not considered a close relative.

Family Pongidae (Congo *mpongi* = chimpanzee, or *mpongo* = fatness) All other great apes, chimpanzee, orangutan, gorilla. Although closer to man than other living creatures, they are not his ancestors.

Family Hominidae (L. *homo* = man) One living species, *Homo sapiens*. Others extinct, e.g., *Homo neanderthalensis*.



Biological Terms

- Aboral** The side opposite the mouth.
- Absorption** The passage of liquid or dissolved substances into cells, through membranes.
- Acid** Any substance producing free hydrogen ions (H^+) in solution.
- Adhesion** A molecular surface force causing unlike molecules to cling together.
- Adrenal gland** An endocrine gland located near the kidney.
- Adrenalin** A hormone produced by the medulla of the adrenal gland.
- Adsorption** The attachment of substances to the surface of others. A molecular phenomenon.
- Adventitious** Arising in unusual places, such as some buds or roots.
- Agglutinin** A substance causing cells or microorganisms in the blood to stick together.
- Alkali** Having the property of a base. Producing free OH^- ions.
- Allantois** An embryonic membrane in birds, reptiles, and mammals, serving for excretion and respiration.
- Allele** One of a pair of contrasting genes on homologous chromosomes through which alternative characteristics are transmitted.
- Allergy** A condition of unusual sensitivity to substances normally harmless.
- Alternation of Generations** Reproduction by alternate sexual and asexual phases in many plants and some animals.
- Altricial** Condition of birds hatched in a helpless condition and confined to the nest for a prolonged period.
- Alveolus** The terminal air-sac of the lung.
- Amino acid** Any of thirty or more organic compounds containing the amino group (NH_2) and the carboxyl group ($COOH$).
- Amnion** Thin, inner embryonic membrane surrounding the embryos of reptiles, birds, and mammals.
- Amniote** A vertebrate with an amnion, including reptiles, birds, and mammals.
- Amoeboid** Like an amoeba, especially with reference to pseudopods.
- Amphoteric** Capable of acting either as a base or as an acid.
- Amylase** A starch-hydrolyzing enzyme.
- Anabolism** Constructive metabolism, in which simpler compounds are converted into more complex ones.
- Anaerobic** ~~Thriving in the absence of oxygen.~~
- Anaphase** The phase in mitosis during which the chromosomes travel from the equatorial plate to the poles.
- Androsterone** A hormone which produces masculinizing properties.
- Anemia** A condition of deficiency of hemoglobin in the blood.
- Angiosperm** Plant with seeds enclosed in an ovary.
- Anion** Any ion carrying a negative charge.
- Antenna** Whip-like segmented sensory organ on the head of an arthropod.
- Anther** That part of the microsporophyll or stamen which produces the pollen.
- Antheridium** Male or sperm-producing structure in the gametophyte generation of lower plants.
- Anthropoid** Man-like, or shaped like man.
- Antibody** Any specific substance produced by an organism which counteracts the effects of foreign substances or organisms.
- Antigen** A substance which when introduced into the body stimulates the production of antibodies.
- Antitoxin** A substance found in the body fluids which counteracts specific poisons or toxins.
- Anus** Posterior terminal opening of the digestive tract.
- Aorta** The main artery of the systemic circuit, springing from the heart.
- Archegonium** The female or egg-producing structure in the gametophyte generation of lower plants.
- Articulation** The junction between two or more bones of the skeleton. A joint.

- Ascospore** A spore produced in an ascus.
- Ascus** A club-shaped spore-sac of the fungi Ascomycetes, usually containing eight spores.
- Assimilation** The processes by which an organism converts substances into its own protoplasm.
- Aster** A star-shaped cytoplasmic structure found particularly in the mitotic figures of animal cells.
- Astigmatism** A defect of the optical system of the eye causing light coming from an external point source to converge unequally in different meridians on the retina.
- Atrium** An external cavity in lower chordates formed by folds of the body wall. Also applied to the auricles of the heart.
- Auricle** The chamber or chambers of the heart which receive incoming blood. Also the flaps on either side of the head of a turbellarian.
- Autocatalysis** The ability of a catalyst to synthesize more of its own substance.
- Autosynthesis** A function characteristic of life in which an organism duplicates, by synthesis, more of its own structure.
- Autotrophic** Self-nourishing. Referring to organisms that do not depend on others for their nutritive processes.
- Auxin** Growth-controlling hormone-like substances produced by plants.
- Avicularia** Tweezer-like individuals of polymorph bryozoan colonies shaped somewhat like the head of a bird.
- Axon** The process of a neuron which conducts impulses away from the body of the neuron.
- Bacillus** A rod-shaped bacterium.
- Bacteria** Simplest organisms, classed as plants.
- Bacteriophage** An autosynthetic substance, possibly living, which destroys bacteria.
- Barbule** The small lateral shaft of a feather.
- Base** An alkali. Any substance producing free hydroxyl ions (OH^-) in solution.
- Basidiospores** Spores produced in a basidium.
- Basidium** The specialized reproducing structure of basidiomycetes formed by the swollen terminal cell of a hypha.
- Basilar membrane** The membrane of the cochlea of the inner ear upon which rest the organs of Corti.
- Bilateral symmetry** That pattern of structure which makes an organism symmetrical with respect to a single plane only, dividing it into right and left halves.
- Bile** The liver secretion, containing salts which aid in emulsification of fats, and products of hemoglobin disintegration.
- Bile duct** The duct leading from the gall bladder to the duodenum.
- Biramous** Forked.
- Blastopore** The opening into the archenteron of the gastrula.
- Blastula** That stage in the early embryos of metazoans where the cells form a hollow sphere.
- Bowman's capsule** The cup-shaped enlargement of a kidney tubule which houses a knot of capillaries, the glomerulus.
- Brachiate** To swing hand over hand in the manner of apes in trees.
- Brachydactyly** A hereditary condition producing short fingers and toes.
- Branchial arch** The cartilaginous or bony arch supporting the gills.
- Budding** A modification of grafting, in which a bud of a desired species is grafted onto the stem of another plant.
- Caecum** A dilated portion at the base of the large intestine into which the small intestine opens.
- Calorie** (Small) The amount of heat required to raise the temperature of one gram of water one degree Centigrade in temperature, at a specified room temperature. The large calorie consists of 1000 small calories.
- Calyx** The outer circle of sepals in a flower.
- Cambium** A layer of undifferentiated cells separating phloem and xylem in vascular plants which by proliferation and differentiation produces increase in thickness of the stem.
- Capillarity** The conduction of liquids through fine vessels by adhesion and cohesion.
- Carapace** A stiffened skin fold growing from the head and extending over the thorax, as in a lobster.
- Carbohydrate** A class of compounds consisting of oxygen, hydrogen, and carbon, with hydrogen and oxygen usually in the proportion of H_2O .
- Carboxyl group** A group of atoms designated by the formula COOH .
- Cardiac** Pertaining to the heart.
- Carnivore** Any flesh-eating organism, especially certain vertebrates.
- Carotid artery** One of the large arteries leading from the aorta to the head.
- Carpel** The pistil or megasporophyll of a seed plant.
- Carpus** The wrist.

- Cartilage** Gristle. An elastic structural material forming the entire skeleton of lower vertebrates and parts of the skeletons of all vertebrates.
- Catabolism** Destructive metabolism, in which larger molecules are broken down into smaller ones.
- Cataract** Any opacity of the lens of the eye or its capsule.
- Cation** A positively charged ion.
- Cell** A unit of protoplasm consisting of nucleus, cytoplasm, and cell membrane. The biological unit of most living organisms.
- Cell membrane** A layer of differentiated cytoplasm forming the outer coating of cells.
- Cell wall** A non-living, secreted structure forming a protective box around many cells.
- Centrifugal force** A force tending to cause a revolving body to flee the center, due to its tendency to continue in a straight line.
- Centrosome** A structure forming the center of a spindle apex or aster in cells undergoing mitosis.
- Cephalisation** The transfer of control to the head of an organism.
- Cephalothorax** The fused head and thorax of arachnoids and higher crustaceans.
- Cercaria** Tailed larvae of the liver fluke.
- Cerebellum** The part of the brain behind the cerebrum and above the medulla.
- Cerebrum** The main portion of the brain in higher vertebrates, consisting of two cerebral hemispheres.
- Cervical** Pertaining to the cervix or neck.
- Chitin** Nitrogenous exoskeletal material of arthropods.
- Chloragen cells** Greenish cells which form the outer coating of the intestinal wall of certain annelids.
- Chlorenchyma** Tissue consisting of chlorophyll-bearing cells in green plants.
- Chlorophyll** The green coloring matter in plants which serves as a catalyst in photosynthesis.
- Chloroplast** A cytoplasmic body containing chlorophyll.
- Chordate** A member of the phylum Chordata, possessing a notochord during at least a part of its life.
- Chorion** The outer embryonic membrane of land vertebrates. In mammals it contributes an important part of the placenta.
- Choroid** The heavily pigmented coat of the eye between sclera and retina; heavily vascular, it supplies food and optical insulation.
- Chromatin** The name applied to the staining substances of which chromosomes are composed.
- Chromatophore** A pigment-bearing cell.
- Chromonema** The thread-like, persisting core of chromosomes.
- Chromosome** The gene-bearing rod-like structure in the nucleus of a cell which forms the characteristic mitotic figures.
- Cilia** Motile hair-like projections produced by many cells.
- Cleavage** The process of embryonic cell division following the zygote stage.
- Clitellum** A glandular thickening of the outer body wall of the earthworm which secretes a cocoon for sperm and eggs.
- Clitoris** The female homologue of the male penis.
- Cloaca** A common duct leading to the outside for excretory, digestive, and reproductive products in many vertebrates.
- Coccus** A spherical form of bacterium.
- Cochlea** The spiral tube of the inner ear, housing the mechanism of sound analysis.
- Coelom** The body cavity in most metazoans, surrounded on all sides by mesoderm.
- Cohesion** Attractive force between molecules of the same kind.
- Colloid** A dispersion of jelly-like consistency consisting of particles too large to pass through differentially permeable membranes, but too small to be microscopically visible.
- Colon** The large intestine, excluding the caecum and appendix.
- Colony** An assemblage of non-differentiated cells which retain their independence but live as a community.
- Columella** A small ossicle of the inner ear of amphibians, reptiles, and birds.
- Commensalism** Mutualism between organisms — not parasitism. Literally "eating at the same table."
- Compound** A substance consisting of two or more different atoms in chemical union.
- Conidium** Externally produced air-borne spore produced by many fungi.
- Conjugation** The temporary sexual union of two cells resulting in the exchange of nuclear material.
- Convergence** Superficial similarity between organisms exposed to similar environmental conditions.
- Copulation** The act of sexual intercourse or coitus.
- Cornea** The transparent anterior layer of the eyeball.

- Corolla** The circle of modified leaves forming the petals of a flower.
- Corpus luteum** The yellow body, left when the Graafian follicle has discharged its ovum. Produces the hormone progesterone.
- Cortex** The outer layer of an organ.
- Cortical hormone** A hormone produced in the cortex of the adrenal gland, and involved in the control of sugar metabolism.
- Corticalization** The process of transferring control of action to the cerebral cortex.
- Cortical system** The cylinder of tissue surrounding the central cylinder or stele of vascular plants.
- Cotyledon** Embryonic leaf of seedling plants.
- Cowper's glands** The bulbo-urethral glands which secrete a viscid portion of the seminal fluid.
- Cretinism** A disease marked by mental and physical retardation, caused by thyroid deficiency.
- Crossing-over** The exchange of gene-bearing segments of homologous chromosomes during synapsis.
- Crystallloid** A dispersion consisting of individual small molecules.
- Cuticle** A tough, outer, non-cellular coating in many animals and plants.
- Cutinize** To produce a tough, non-cellular pellicle on the surface of skin.
- Cytoplasm** Collective term for that part of protoplasm outside the nucleus.
- Deciduous** Falling or shedding periodically, as the leaves of deciduous trees in fall.
- Dendrite** The branching processes leading nervous impulses towards the neuron cell body.
- Dermal system** The outermost covering of the stem in vascular plants.
- Dermis** The inner tissue layer of vertebrate skin.
- Diabetes** A disease marked by excessive secretion of urine. Usually diabetes mellitus, in which there is an inability to oxidize carbohydrates, due to failure of the pancreatic Islands of Langerhans and resulting in excretion of sugar in the urine.
- Diaphragm** The muscular partition between the pleural and peritoneal cavity of mammals.
- Diastole** The dilation phase of the heartbeat cycle.
- Dicotyledonous** Used of plants having two seed-leaves or cotyledons.
- Diffusion** The process whereby particles scatter from a region of greater concentration to one of lesser concentration.
- Digestion** The hydrolyzing process that occurs in the alimentary tract, transforming foods into soluble form.
- Diploblastic** Consisting of two primary tissue layers.
- Diploid** Having a double number of chromosomes or two "sets" as in a zygote and in the cells produced from it by mitosis.
- Dispersion** A system in which some discontinuous substance is scattered throughout a continuous medium.
- Diuretic** Tending to increase the excretion of urine.
- Diuretic hormone** A hormone produced by the posterior pituitary gland and controlling water balance in the body.
- Dominant** Term referring to one of a pair of alleles which dominates in effect over the other.
- Dormancy** A state of prolonged sleep-like condition with lowered metabolism.
- Dorsal** Pertaining to the back.
- Drive** An inherent force which activates instinctive behavior.
- Drone** A male bee.
- Drupe** Fleishy fruit with a single, stony inner seed, such as the cherry.
- Duct** A conducting tube leading from one part of an organism to another.
- Duodenum** The anterior portion of the small intestine, just posterior to the stomach.
- Dyad** Two associated chromatids passing to the same pole during meiosis.
- Dynamic** Pertaining to forces not in equilibrium, or to motion.
- Dysgenic** Tending to cause genetic deterioration in a species.
- Ecology** That branch of biology which deals with the relationship between organisms and their environment.
- Ectoplasm** The outer, less fluid portion of the cytoplasm of the cell. Sometimes visibly differentiated from the endoplasm.
- Egest** To eliminate indigestible waste from the alimentary tract.
- Elate** An elastic filament which assists in the dispersal of spores.
- Electrolyte** A substance which dissociates into ions when in solution and hence carries an electric current.
- Electron** The unit negatively charged particle of an atom which revolves about the nucleus.

- Element** A substance consisting of only one kind of atom, and hence not reducible into simpler form by ordinary chemical means.
- Elephantiasis** A chronic disease of the lymphatic channels caused by filaria. It produces thickening and ulceration of the skin.
- Embolus** A plugging blood clot brought from another point to a smaller blood vessel.
- Embryo** The immature organism during its development from zygote to full organization.
- Embryology** The science of the beginning or undeveloped stages of living organisms, or the process of early development.
- Embryo sac** The female gametophyte of the seed plant.
- Emulsion** A dispersal of one liquid, in the form of droplets, in another continuous liquid, where the two liquids are not miscible.
- Endocrine** Referring to the glands of internal secretion.
- Endoderm** The innermost of the three germ layers of triploblastic organisms.
- Endoskeleton** An internal skeleton, as in vertebrates.
- Endosperm** The food-storage tissue of the seed in seed plants.
- Endostyle** A ciliated groove of the ventral pharynx of lower chordates.
- Enteron** The alimentary canal.
- Enzyme** An organic catalyst or ferment.
- Epicotyl** The part of the shoot above the cotyledons.
- Epidermis** The outer cell layer of the skin.
- Epiphysis** The terminal end of a long bone in immature organisms, separated from the main shaft by cartilage.
- Epiphyte** A plant which grows upon the body of another, but is not parasitic thereon.
- Ergot** A fungus affecting the seeds of certain cereals, especially rye. Also the drug derived from the plant which causes contraction of smooth muscles.
- Erosion** The process by which land surface is worn away by the action of wind, water, and temperature change.
- Erythrocyte** A red blood cell.
- Esophagus** The food pipe, from pharynx to stomach.
- Estrogen** An estrus-producing substance. The female hormonal counterpart of the male testosterone. Produced by follicle and stimulates pituitary gland.
- Estrus** The mating period in female mammals, characterized by intensified sexual urge.
- Etiolation** The paleness and abnormal elongation of plants grown in the absence of light.
- Eugenics** The science of race-improvement through genetic improvement.
- Eunuch** A castrated human male.
- Euthenics** The science of race improvement through the agency of improved environment.
- Evaporation** The process by which liquids or solids turn into vapor and pass off into the air.
- Evolution** The theory that complex organisms have derived from simpler ones.
- Excretion** The elimination of soluble waste, as by the kidneys.
- Exophthalmia** Abnormal protrusion of the eyeballs, often associated with hyperactive thyroid glands.
- Exoskeleton** An external skeleton, as in arthropods.
- Extensor** A muscle causing extension or straightening of a member.
- Fallopian tube** The oviduct, leading from ovary to uterus.
- Fascia** A sheet or band of tissue which invests a muscle.
- Fat** Organic compound of carbon, hydrogen, and oxygen, but little of the latter. Fats are compound esters of fatty acids with glycerol and are greasy to the touch.
- Fatty acid** An organic acid consisting of a long string of carbon atoms with attached hydrogen, and a carboxyl radical at one end. Combined with metallic salts they form soap; with glycerol, they form fats.
- Fault** A break in the continuity of a body of rock, with a change in elevation between the two halves.
- Fauna** Collective term for the animals of a given region or period.
- Feces** Indigestible egested matter.
- Fertilization** The union of the sperm cell with the egg.
- Fetus** Embryo in egg or womb. Human embryo after the third month.
- Filament** Any slender, stalk-like, cellular structure.
- Filiariasis** A lymphatic disease caused by the presence of the nematode Filaria. See also elephantiasis.
- Filterable virus** Complex nucleoprotein molecules or simple living organisms capable of reproduction within the tissues of other organisms

- only, causing disease. Visible only by electron microscope.
- Fin* Membranous locomotor structure of fishes, and some other aquatic organisms.
- Flagellum* Motile, whip-like projection found in many cells.
- Flame cells* Ciliated excretory structures found in some lower organisms, as in Planaria.
- Flexor* Any muscle causing a bending or flexion of a member.
- Flora* Collective term for the plants of a given region or period.
- Flower* The reproductive organs and their appendages in seed plants.
- Follicle* A small secretory sac or gland. Hair follicle. Graafian follicle in which ova are produced.
- Fontanelle* An unossified spot in the cranium of a young child.
- Fossil* Any mineralized visible record of life of past ages.
- Fovea* A depression, especially the fovea centralis in the retina of the eye, region of keenest vision.
- Fruit* The developed ovary and associated parts of seed plants in which the seeds are housed.
- F.S.H.* Follicle-stimulating hormone.
- Fungus* Any thallophyte of the subclass Fungi. Molds, rusts, and toadstools.
- Galaxy* A spiral nebula, e.g., the Milky Way.
- Gametangium* Structure which produces gametes, as in Vaucheria.
- Gamete* Any cell of sexual reproduction, as sperm or egg.
- Gametocyte* The state of maturation of gametes in meiosis following the gonia.
- Gametophore* An umbrella-shaped structure bearing archegonia in Marchantia.
- Gametophyte* That phase of plant reproduction in higher plants which produces gametes.
- Ganglion* Collection of nerve cell bodies.
- Gastric caeca* Intestinal out-pocketings in insects.
- Gastro-vascular* Pertaining to the diffuse distributing digestive tract of simple metazoans, such as coelenterates and flatworms.
- Gastrula* That stage in cleavage in which the organism is a double-walled cup of ectoderm and endoderm.
- Gel* A firm colloid, containing much enmeshed liquid.
- Gemmule* Multicellular, internal bud produced by sponges. Surrounded by impervious coats, it can survive hard times.
- Gene* The unit determiner of hereditary traits.
- Genital* Pertaining to the reproductive organs.
- Genotype* Refers to the genetic constitution of an organism.
- Geotropism* Growth reaction of a plant to the gravitational field of the earth.
- Germ plasm* The name applied to cells restricted to reproductive purposes.
- Gill* A vascular respiratory structure of aquatic animals.
- Gill slits* Paired openings from sides of pharynx through body wall. In all chordates at some stage.
- Gizzard* A tough muscular sac in the alimentary tract of birds and some other organisms, serving for maceration of food.
- Gland* An organ specialized for secretion.
- Glaucoma* A disease of the eye, sometimes hereditary, marked by intra-ocular pressure and resulting in blindness.
- Glochidium* A late larval stage of mussels. Parasitic on fishes.
- Glomerulus* The knot of capillaries located in the Bowman's capsule of a kidney tubule.
- Glottis* That part of the larynx associated with vocalization.
- Glucose* Dextrose. A simple sugar.
- Glycerol* A syrupy liquid, chemically, a triatomic alcohol. With fatty acids it forms fats.
- Glycine* A simple amino acid. Amino-acetic acid.
- Glycogen* A polysaccharide formed in the liver. Animal starch.
- Goiter* A swelling of the thyroid gland often caused by iodine deficiency.
- Golgi bodies* Granular structures of uncertain function found in cells.
- Gonad* Reproductive gland, ovary or testis.
- Gradient* A graded change in concentration or distribution of a substance within a medium from point to point.
- Grafting* The process of transplanting tissue from one part of an organism to another, or from one organism to another.
- Gray matter* That part of the spinal nerve cord and brain containing the neurons and their synapses.
- Growth hormone* A hormone produced by the anterior pituitary gland. Lack of it causes dwarfing; excess causes gigantism.
- Guard cell* One of the cells surrounding the stomata or air-pores in leaves.
- Gymnosperms* Plants that produce naked seeds, such as the pine.

- Habit** An acquired reflex action.
- Halteres** Rudimentary wing-structures, looking like knobbed rods, serving as balancers in dipteran insects.
- Haploid** Having only a single set of chromosomes, as in gametes.
- Hauastoria** Specialized rootlets of certain parasitic plants, which penetrate to the vascular bundles of the host plant, as in mistletoe.
- Haversian system** A system of concentric bone layers surrounding an extensive canal system, characterizing the bony structure of the dense bone of vertebrates.
- Heart** A muscular organ which pumps blood.
- Heat** Condition produced by the random movements of molecules in a substance.
- Heliotropism** A directional growth response of plants with respect to light.
- Heme** The non-protein, iron-bearing constituent of hemoglobin.
- Hemocoel** Body cavity in which blood circulates, as in arthropods.
- Hemocyanin** A blue, copper-bearing oxygen-carrying substance found in the blood of arthropods and mollusks.
- Hemoglobin** The oxygen-carrying red pigment of red blood cells, consisting of the protein globin combined with heme.
- Hemophilia** Hereditary, sex-linked disease marked by failure of blood to clot.
- Herbaceous** Pertaining to non-woody plants.
- Herbivore** Any animal subsisting wholly on plant food.
- Heredity** The transmission of hereditary characters from parents to progeny.
- Hermaphrodite** An individual possessing both male and female reproductive structures.
- Heterotrophic** A form of nutrition not self-sustaining, due to inability to synthesize proteins and carbohydrates from inorganic substances.
- Heterozygous** The state of an organism containing conflicting members of a pair of alleles.
- Holophytic** The green-plant type of nutrition, based upon photosynthesis.
- Holozoic** Animal type of nutrition based upon the ingestion of organic foods.
- Homology** Fundamental similarity of structures due to common origin, though possibly modified for wholly unlike purposes.
- Homozygous** The state of an organism containing only the same members of a pair of alleles.
- Hormone** A chemical substance produced by a gland which produces a specific coordinating effect at some other point.
- Huntington's chorea** A degenerative hereditary disease of the brain structure.
- Hybrid** An organism resulting from the crossing of two species.
- Hydrolysis** The chemical splitting of compounds by interaction with water.
- Hydrophyle** Plants adapted to life in the water.
- Hydroxyl ion** The OH⁻ ion, conferring the property of a base or alkali.
- Hyphae** Thread-like elements of the mycelium of a fungus.
- Hypertonic** Denoting a solution with a greater concentration of non-diffusible molecules than the one to which it is compared.
- Hypocotyl** That part of the embryo seedling which lies below the cotyledons.
- Hypothalamus** The ventral subdivision of the diencephalon. An important regulatory center of the brain, as in control of body temperature.
- Hypotonic** Denoting a solution with a lesser concentration of non-diffusible molecules than the one to which it is compared.
- Ichthyosis** A disease characterized by dryness and scalliness of the skin.
- Igneous** Produced under conditions of intense heat, as igneous rock.
- Imago** The adult form of an insect.
- Incisor** Any one of the four front cutting teeth in either jaw.
- Incus** The middle bone of the three small ossicles of the inner ear. The anvil.
- Independent assortment** Expressing the principle that the assortment of any one pair of chromosomes at maturation is not influenced by any other pair.
- Indusium** A membrane covering the sporangia of a fern.
- Inertia** The tendency of an object to maintain its state of motion or rest unless acted upon by an outside force.
- Inflorescence** The flowering part of a plant.
- Ingest** To take food into the alimentary tract.
- Inhibit** To arrest or restrain a process.
- Inorganic** Most compounds not containing carbon. Compounds not resulting exclusively through the activities of living organisms.
- Insectivorous** Insect-eating.
- Insemination** The act of depositing seminal fluid in the female reproductive tract.

- Instinct** An inherited chain of reflex actions resulting in unlearned complex behavior.
- Insulin** The hormone produced by the Isles of Langerhans in the pancreas which make possible normal sugar metabolism.
- Integument** The outer sheath skin, or covering of an organism.
- Interphase** The condition of a cell between mitotic divisions.
- Intestine** The membranous digestive tube that extends from stomach to anus.
- Invaginate** The infolding of a tissue so as to become ensheathed.
- Invertebrate** Any organism not having a vertebral column.
- Ion** An electrically charged atom, radical, or molecular fragment, formed by the loss or gain of one or more electrons.
- I.Q.** Intelligence quotient. A number assumed to express the mental capacity of an individual.
- Iris** A circular pigmented membrane in front of the lens of the eye, with a circular perforation, the pupil, in the center.
- Irritability** The capacity of a living structure or organism to respond to a stimulus.
- Isles of Langerhans** The glands in the pancreas which secrete insulin.
- Isogamy** A state in which the gametes are not sexually differentiated.
- Isolation** The segregation of one organism or species from another.
- Isotonic** Denoting a solution with the same concentration of nondiffusible molecules as the one to which it is compared.
- Isotope** A chemical element having the same properties as another, but differing by one or more units in atomic weight.
- Jaundice** A condition in which bile is absorbed into the blood stream, causing yellow pigmentation of the skin.
- Kinesthetic** Pertaining to the sense perception of muscular movement, position, and weight.
- Kinetic energy** Energy of motion, contrasted to potential energy.
- Kinetochore** A specific point on a chromosome to which a spindle fiber becomes attached during mitosis.
- Labial** Pertaining to the lips.
- Labium** Lip. The lower lip of arthropods.
- Labrum** Upper lip of arthropods.
- Labyrinth** A lymph filled sac, which in higher vertebrates is transformed into semi-circular canals, utricle, saccule and cochlea.
- Lactation** Milk production.
- Lacteal** A fine tube-like blind pocket of the lymphatic system that extends into each villus of the intestine.
- Lactose** Milk sugar, disaccharide.
- Lacuna** Any small pit, hollow, or depression. Applied to the spaces in the Haversian system of bone in which lie the bone cells.
- Lamella** One of the concentric layers of bone spicules produced in the Haversian system of bone.
- Lanugo** Fine downy hair growth found on the body of a fetus.
- Larva** Free-living embryonic stage in animals undergoing metamorphosis, such as a caterpillar or a tadpole.
- Larynx** That part of the trachea containing the vocal cords.
- Lateral** To the side.
- Legume** Any one of a family of plants including peas, beans, clover, and vetch.
- Lens** The light-refracting body behind the iris of the eye.
- Leukocyte** White blood cell, colorless and amoeboid.
- L.H.** Luteinizing hormone which induces ripening of the follicle.
- Lichen** A symbiotic growth consisting of an alga and a fungus.
- Ligament** Fibrous connective tissue that joins bones.
- Light year** The distance that light travels in one year.
- Lignin** An organic compound which with cellulose forms the bulk of the woody structure in plants.
- Linkage** Tendency of closely spaced genes on a chromosome to be handed down as a unit.
- Lipase** A fat-splitting enzyme.
- Lipoid** Fat-like, of a lipid. Includes fats, fatty acids, waxes, and soaps.
- Liver** A large glandular organ in vertebrates which functions as a processing organ for many foods brought to it through the bloodstream.
- Liverworts** Primitive members of the phylum Bryophyta. The Hepaticae.
- Lumbar** Pertaining to the region of the back between the pelvis and the lower ribs.

- Lung** The organ of gas exchange or respiration in most air-breathing animals.
- Lymph** Blood plasma which bathes the tissues and returns to the blood stream through the lymphatic system of ducts.
- Lysin** An antibody causing dissolution.
- Macronucleus** The larger of the two nuclei found in most ciliates.
- Malleus** The first of the three ossicles of the inner ear, the hammer.
- Malpighian tubules** Thread-like excretory structures in insects.
- Mammal** Animal which suckles its young with milk.
- Mandible** A mouth part. Variously modified for chewing and sucking in arthropods. Applied to the skeleton of the lower jaw in vertebrates.
- Mantle** An enveloping fold of the body wall which surrounds the body proper, as in mollusks. In some it secretes a shell.
- Marsupial** Primitive mammals, most of them indigenous to Australia, characterized by a ventral brood pouch or marsupium.
- Mass** That property of matter which determines its inertia. Mass is directly proportional to its weight.
- Mastax** The jaws or chewing mill of rotifers.
- Maturation** Applied to the ripening or maturing divisions of germ cells in meiosis.
- Maxilla** A mouth part. There are two pairs in crustaceans, one in insects. Applied to the skeleton of the upper jaw in vertebrates.
- Medulla oblongata.** The anterior terminal portion of the spinal nerve cord merging with and constituting a portion of the brain. It lies just below the cerebellum.
- Medusa** A jellyfish.
- Megaspore** The larger spore in heterosporous organisms. An ovule in seed plants.
- Meiosis** The sequence of maturation divisions resulting in gamete maturation.
- Meissner's corpuscle** A tactile receptor in the skin.
- Membrane** A thin layer of tissue or modified cytoplasm which forms a surface layer and divides one region from another.
- Menstruation** The periodic sloughing of epithelial uterine tissue, accompanied by hemorrhage, in the human female.
- Meristem** Undifferentiated growing tissue in vascular plants.
- Mesencephalon** Midbrain.
- Mesenchyme** Undifferentiated embryonic tissue.
- Mesentery** A double fold of peritoneal tissue which attaches the intestine to the body wall.
- Mesoderm** The intermediate layer of body tissue in triploblastic animals.
- Mesoglea** A non-cellular layer between ectoderm and endoderm in coelenterates.
- Mesonephros** Mid-kidney. The second phase of kidney development in vertebrates, becoming the final functioning kidney in fishes and amphibians.
- Metabolism** The sum total of constructive and destructive chemical changes within the tissues of an organism. It does not include digestion.
- Metamerism** The segmental scheme of body structure seen in many metazoans.
- Metamorphosis** A radical change in the structure of an animal during its process of maturation; caterpillar to butterfly, tadpole to frog.
- Melanephros** The final phase of kidney development, becoming the permanent kidney in reptiles, birds, and mammals.
- Metaphase** That phase of mitosis during which the chromosomes are still in contact on the equatorial plate of the cell.
- Metapleural folds** The outer skin folds forming the atrium in Amphioxus.
- Metazoa** Many-celled animals.
- Micron** The one-thousandth part of a millimeter.
- Microspore** A small spore in a heterosporous organism. A pollen grain.
- Migration** The mass movement of organisms or tissues from one region to another.
- Mimicry** The resemblance of one organism to some other animate or inanimate structure, usually bringing advantage to the mimic.
- Mitochondria** Granular rod-like or thread-like enzymatic structures found in all cells.
- Mitosis** The usual process of somatic cell division, during which chromatic material is exactly duplicated and evenly distributed between the two newly formed daughter cells.
- Molecule** A unit composed of two or more joined atoms. The smallest unit of a compound that still retains the properties thereof.
- Monocotyledonous** Used of plants having but one seed leaf.
- Monosaccharide** A simple sugar consisting of a single chain of carbon atoms. The term includes sugars other than the simple hexoses.
- Monozygotic** Pertaining to organisms derived from a single zygote. Monozygotic or identical twins.

- Morula** The "mulberry" phase of an embryo in early cleavage, consisting of a spherical clump of relatively few cells.
- Mosaic vision** The type of vision achieved by the compound eyes of arthropods.
- Mucin** A slimy gluco-protein secretion of the mucous membranes.
- Müllerian duct** An embryonic duct which ultimately becomes transformed into oviduct and uterus in the female vertebrate.
- Mutant** An organism carrying a new gene structure or mutation.
- Mutation** A random, persistent change in gene structure.
- Mutualism** A relationship bringing mutual benefit, as between insects and flowers in pollination.
- Mycelium** The matted network of hyphae which constitutes the body of a fungus.
- Mycorrhiza** Symbiotic fungi growing on the roots of vascular plants.
- Myofibril** A slender contractile fiber in muscle cells.
- Myopia** Near-sightedness.
- Myotome** A somite. One of the segmental tissue blocks which develop along the vertebral column of vertebrates and persist in lower ones.
- Myxedema** A disease caused by subnormal functioning of the thyroid gland, resulting in general puffiness and subnormal mental activity.
- Natural selection** The process of elimination of the unfit by natural processes.
- Nauplius** A larval stage characteristic of many crustaceans.
- Nematocyst** The explosive capsule and thread within the cnidoblasts of coelenterates. The active portion of the nettle cells.
- Nephrostome** A ciliated funnel-like opening of a kidney tubule.
- Nephrotome** A tissue strip in the early embryo from which the nephridia develop.
- Neural crest** A band of cells lying along the neural fold of vertebrates which give rise to the neurons of cranial and spinal ganglia.
- Neural plate** That region of the early vertebrate embryo which produces the nerve cord.
- Neuroblast** A cell which differentiates into neurons.
- Neuroglia** The supporting tissue of nervous structures.
- Neuron** A nerve cell
- Neutron** A neutral unit structure of matter with approximately the same mass as a proton.
- Nitrate bacteria** Soil bacteria which transform nitrites into nitrates.
- Nitrite bacteria** Soil bacteria which transform ammonia into nitrites.
- Non-disjunction** Failure of allelomorphous chromosomes to separate during reduction divisions of meiosis.
- Non-polar compound** A compound, usually formed by sharing, with symmetrical distribution of electrical charges, hence not forming poles. Common in fats and oils.
- Notochord** The unsegmented elastic rod that forms a skeletal axis in chordates. It persists in lower forms but disappears in the higher.
- Nucellus** The central portion of the ovule which encloses the embryo sac in the flowers of seed plants.
- Nucleolus** A sharply defined body found in the nuclei of many cells. Of uncertain function.
- Nucleoplasm** The protoplasm constituting the nuclear mass of cells.
- Nucleoprotein** A complex protein consisting of nucleic acid and simple proteins, constituting the protein of cell nuclei.
- Nucleus** The inner kernel of a structure. The inner mass of an atom, consisting of protons and neutrons. The inner protoplasmic mass of a cell.
- Nutrition** The process of ingestion, digestion, and assimilation of foods for energy, growth, and repair.
- Ocellus** The simple eye of some invertebrates.
- Olfactory** Pertaining to the sense of smell.
- Ommatidium** The single element of a compound eye of an arthropod.
- Ontogeny** The development of an individual organism from egg through embryonic stages.
- Oocyst** A multiplication phase following the zygote in the life cycle of the malarial parasite.
- Oocyte** An immature ovum, during meiosis, following the gonial stage.
- Oogamy** Reproduction by true eggs and sperm.
- Oogenesis** The maturation process of egg cells.
- Oogonium** The multiplication phase of immature ova in meiosis.
- Operculum** Any structure serving as a lid or cover. The cover over the gills of fishes.
- Oral groove** A spiral groove leading to the gullet of certain ciliates.
- Organelle** The organ-like structures in protozoans.
- Organic** Pertaining to or produced exclusively through the activities of living organisms.

- Organiser** A hormone-like substance in early embryonic development which influences the growth and differentiation of cell regions.
- Organ of Corti** The sound-analyzing structure of the cochlea of the ear.
- Orthogenesis** Former belief that species evolve along predetermined lines.
- Osmosis** Movement of a substance — usually water — through a differentially permeable membrane.
- Ossification** Transformation into bone.
- Osteoblast** Cells that build bone tissue.
- Osteoclast** Cells that destroy bony structure.
- Ovary** The female gonad, which produces egg cells.
- Oviduct** The tube leading from the ovaries to the uterus or to the outside of the organism.
- Oviparous** Reproducing by the laying of eggs.
- Ovoviviparous** Reproducing by eggs which hatch before laying. Hence a form of live birth.
- Ovulation** The act of producing eggs.
- Oxidation** To combine with oxygen, liberating energy, often in the form of heat.
- Palaeontology** The science dealing with the life of past geological periods through a study of fossils.
- Palisade cell** One of the elongated chlorenchyma cells often forming layers near the surface of green leaves.
- Palps** Abbreviated tactile appendages attached to the maxillae of arthropods.
- Parthenogenesis** Reproduction by the development of an egg without fertilization.
- Pancreas** A diffuse digestive gland lying on the mesentery of the duodenal loop. Its enzymes pass into the duodenum by the pancreatic duct.
- Pangene theory** A theory proposed by Darwin, but now not accepted, to explain the supposed inheritance of acquired characteristics.
- Papillus** A small finger-like projection, e.g., the dermal papillae.
- Parasite** An organism which lives on or in another and at its expense.
- Parathormone** The hormone produced by the parathyroids which functions in control of calcium metabolism.
- Parathyroids** The four small glands lying on the thyroid gland. They produce a hormone functioning in calcium metabolism, parathormone.
- Parenchyma** Fundamental tissue in plants, consisting of unspecialized cells, and serving for storage or synthesis of foods, as in the leaves.
- Pathogen** An organism producing disease.
- Pectoral** Pertaining to the breast or chest.
- Pedicellaria** Minute stalked pincers on the outer surface of echinoderms.
- Pellicle** A thin non-living membrane or sheath produced by some animal cells.
- Pelvic** Pertaining to the basin-like cavity in the lower part of the trunk of vertebrates, the pelvis.
- Penicillin** The active anti-bacterial substance produced by the mold *Penicillium*.
- Penis** The male copulatory organ.
- Pepo** Modified type of berries with a hard shell outside the fleshy portion, such as a squash or melon.
- Pepsin** A protein-splitting enzyme produced in the stomach.
- Peptid linkage** A pattern of chemical union by which amino acids are often joined to form proteins. A link is formed between the amino radical of one amino acid and the carboxyl group of another.
- Perennial** Persisting for more than one year.
- Pericardium** A membranous sac which surrounds the heart.
- Perichondrium** A connective tissue sheath surrounding cartilage.
- Periosteum** A tough fibrous membrane surrounding bone and capable of bone building.
- Peristalsis** Progressive wave-like contractions of the walls of a tube, frequently the alimentary tract.
- Peritoneum** The serous membrane which lines the peritoneal or coelomic cavity of vertebrates and surrounds all contained organs.
- Permeability** Referring to the degree to which a membrane permits substances to pass through it.
- Petal** A modified leaf forming part of the corolla of a flower.
- Petiole** A slender leaf-stalk by which the leaf is attached to the stem.
- Phagocyte** A cell capable of ingesting solid bodies by pseudopods.
- Pharynx** The anterior portion of the alimentary tract between mouth and nose and esophagus.
- Phase reversal** A change in the relationship of the phases in a dispersion, especially in an emulsion, so that the continuous phase becomes the discontinuous, and vice versa.
- Phenotype** Pertaining to the appearance rather than to the genetic constitution of an individual. Contrasted with genotype.

- Phloem** The outer region of the vascular system of vascular plants, consisting of sieve tubes, companion cells and other tissues, and serving for the conduction of solutions bearing organic compounds.
- Photon** A unit quantum of light.
- Photosynthesis** The chemical process whereby green plants combine carbon dioxide and water with the aid of chlorophyll and the energy of sunlight to produce sugar and give off oxygen as a waste.
- Phylogeny** The evolutionary history of a species.
- Phylum** Primary division of the animal and vegetable kingdoms.
- Physical change** A change in matter which does not involve a change in molecular structure, e.g., water to steam.
- Physics** The science dealing with the properties and interactions of matter other than those dealing with chemical change.
- Physiology** The study of the functioning of organisms.
- Pigment** Any coloring matter deposited in the tissue of the body.
- Pistil** Collective term for ovary, style and stigma of seed plants.
- Pith** The central mass of stems of vascular plants, consisting of large, thin-walled parenchymal cells.
- Pituitary gland** (Hypophysis) An important endocrine gland attached to the base of the brain.
- Placenta** An absorbent, flat structure of higher mammals, consisting of highly vascular embryonic and maternal tissue, and establishing nutritive connection between mother and embryo.
- Placoid scales** Plate-like scales such as those forming the outer covering of sharks.
- Plankton** Collective term for the small animals and plants that float near the surface of water.
- Planula** A ciliated larva of certain lower organisms, as in some coelenterates.
- Plasma** The liquid portion of the blood, excluding blood cells.
- Plasmodium** A mass of protoplasm formed by the fusing of individual amoeboid units.
- Plasmolysis** Contraction or shrinking of cells due to water loss by osmosis.
- Plasmosol** The relatively liquid or streaming part of cytoplasm within a cell.
- Plastid** A specialized body of protoplasm in the cell, as a chloroplast.
- Pleura** A serous mesodermal membrane that covers the lungs and lines the pleural or lung cavity.
- Plumule** The leafy bud of a seedling within a seed, located above and between the cotyledons.
- Polar body** One of the three abortive eggs produced in the maturation of an ovum.
- Polar compound** Any compound with a molecular structure causing uneven distribution of electrical charges. Water and most water soluble substances are polar.
- Polarity** Showing difference of charge or reaction between two ends.
- Pollen** The microspores of seed plants.
- Pollen tube** The long slender tube of the male gametophyte of seed plants, produced by the germinating pollen grain.
- Pollination** The act of transporting pollen from anther to stigma.
- Polychemia** Abnormal increase in red blood cells in the blood.
- Polymorph** Of many forms. Applied to the variously specialized individuals of certain colonial organisms.
- Polyp** A name applied to the sedentary phase of certain coelenterates, such as those building coral reefs.
- Polyloid** Containing more than the normal double set of chromosomes as in most zygotes.
- Polysaccharide** Any carbohydrate composed of more than three monosaccharides or simple sugars chemically joined. Starch, cellulose, glycogen.
- Pome** Fleshy fruit consisting largely of the enlarged receptacle, e.g., apple.
- Pons** A region of the brain consisting of fibers connecting the halves of the cerebellum and joining the midbrain and medulla.
- Portal system** A system of blood vessels beginning and ending in capillaries, as in the hepatic and renal portal systems.
- Potential energy** Energy of position or structure, which may be transformed into kinetic energy.
- Precocial** Applied to birds which are able to move about freely when hatched. Contrasted with altricial.
- Predaceous** Applied to organisms preying upon other animals.
- Primate** Any mammal belonging to the order Primates, which includes lemurs, monkeys, apes, and man.
- Primitive streak** A linear ectodermal thickening produced in the process of gastrulation in birds and mammals, which gives rise to mesoderm.
- Proboscis** An elongated, flexible snout or feeding organ, as in bees and elephants.

- Progesterone** A hormone of the corpus luteum which prepares the lining of the uterus for implantation of the embryo.
- Proglottid** One of the segments of a tapeworm.
- Prognathous** Having protrusive jaws.
- Pronephros** The primordial kidney. The first of three nephridial structures to appear in the embryos of higher vertebrates.
- Prophase** The first phase of mitosis, during which the chromosomes become organized and until they are arrayed on the equatorial plate.
- Proprioceptor** A sensory structure which serves to inform the organism of movement and position of its body.
- Prosencephalon** The forebrain.
- Prostate** A male gland surrounding the neck of the bladder and the urethra.
- Protease** A protein-digesting enzyme.
- Protein** Compound of linked amino acids. An essential ingredient of all protoplasm and characterized by containing nitrogen.
- Prothallus** The gametophyte phase of the reproductive cycle of ferns.
- Protista** Collective term relating to single celled animals and plants.
- Proton** A unit of atomic structure carrying a unit positive electrical charge.
- Protonema** The filamentous, primitive structure usually first produced by the germination of the spore in certain bryophytes.
- ✓ **Protoplasm** The viscid, granular material common to all living organisms, alone displaying the properties associated with life.
- ✓ **Protozoa** One-celled animal organisms.
- Protochula** Larva of marine flatworms.
- Pseudopod** A temporary protrusion of a portion of the protoplasm, as in certain Protozoa, especially the amoeba.
- Pteridosperm** Fossil seed-fern.
- Ptyalin** A starch-splitting enzyme found in the saliva.
- Pulmonary** Pertaining to the lungs.
- Pupa** An intermediate stage in the development of an insect between larva and imago; often immobile.
- Pylorus** The aperture between stomach and intestine, guarded by valve-like circular muscles.
- Race** A variety or subspecies.
- Radical** Usually a group of atoms within a molecule which behaves like a unit. Such as NH_2 , OH , etc.
- Radula** A rasping organ in the mouth, peculiar to many mollusks.
- Recapitulation** A theory suggesting that the ontogeny of an organism may present an abbreviated history of its phylogeny.
- Recessive** Applied to a hereditary character which does not express itself in the presence of its dominant allele.
- Redia** One of the stages in the development of a fluke, produced either from a sporocyst or from another redia.
- Reduction** Chemically, the converse of oxidation, i.e., the removal of oxygen or addition of hydrogen. Also that phase in meiosis in which there is a reduction in the kinds of chromosomes of the gametocyte.
- Reflex** An automatic reaction in animals involving lower nerve centers.
- Renal** Pertaining to the kidneys.
- Respiration** The gas exchange of a cell, taking in oxygen and giving off carbon dioxide. Also the process of lung ventilation.
- Retina** The light-sensitive, inner layer of the eyeball.
- Rh factor** The Rhesus factor. A genetically induced chemical factor found in the blood of some individuals.
- Rhizoid** Root-like structures of simpler plants, either single-celled or consisting of cells strung end to end.
- Rhizome** An underground stem having root-like functions, as in ferns.
- Rhodopsin** Visual purple. A chemical substance produced in the retina and associated with vision.
- Rhombencephalon** The hindbrain.
- Rootcap** A cap of expendable cells produced as a protective sheath over the tip of a growing root.
- Root hair** One of the hair-like absorptive projections of the epidermal cells of a young root found a short distance behind the growing tip.
- Rumen** A large storage-stomach in cud-chewing animals or ruminants.
- ✓ **Rust** A fungus disease attacking cereals.
- Sacculle** The smaller of two sacs of the membranous labyrinth of the inner ear.
- Sacroiliac** The juncture between the sacrum (five fused vertebrae) and the ileum of the pelvic girdle in man.
- Sagittal** Pertaining to a plane running from front to back in bilaterally symmetrical organisms.

- Salt** Any compound produced by the interaction of a base with an acid, such as sodium chloride, common table salt.
- Saprophyte** Plant organism living upon dead organic matter and obtaining its food in soluble form.
- Sarcolemma** The tubular sheath of a muscle fiber.
- Sarcoplasm** The cytoplasmic mass in which the fibrils of the striated muscle are imbedded.
- Saurian** Pertaining to the lizards.
- Schizophrenia** Split personality. A cleavage of mental functions.
- Sclera** Outer supporting coat of the eyeball.
- Sclerenchyma** Supporting tissue in plants composed of thick-walled cells.
- Scurvy** A deficiency disease caused by the lack of vitamin C.
- Sea squirt** An ascidian or urochordate.
- Sebaceous gland** Glands of the skin secreting a lubricating substance, sebum.
- Secretin** A hormone produced by stomach or intestine, controlling secretion of digestive enzymes.
- Seed** The disseminating unit of seed plants, consisting of an embryonic sporophyte surrounded by food supplies and protected by seed coats.
- Segregation** Pertaining to the separation of alleles during the reduction division of meiosis.
- Selection** Applied to the process of breeding by chosen individuals.
- Semicircular canals** The three curved canals in the labyrinth of the inner ear functioning in the control of equilibrium.
- Seminal receptacle** A receptacle for the storage of sperm cells received from another organism during copulation.
- Seminal vesicle** A structure in male organisms for storage of mature sperm before copulation.
- Serosa** Any serum-secreting membrane, such as those lining the body cavities.
- Serum** The clear portion of any animal liquid, especially of blood.
- Sessile** Living attached to a fixed place.
- Setae** Stiff hairs or bristles, as in the earthworm.
- Sex chromosomes** A pair of chromosomes (X and Y) especially concerned with the determination of sex.
- Sexual reproduction** Reproduction initiated by the fusion of two gametes.
- Sieve tubes** Sugar-conducting cells in vascular plants. Adjoining cells achieve protoplasmic continuity through sieve-like perforated end walls.
- Siliceous** Containing or consisting of silica.
- Sinus** A cavity or hollow space. Especially the air cavities of the cranial bones.
- Siphon** A projecting tubular structure in animals through which water is pumped in or out.
- Smut** Fungus producing diseases in plants.
- Sol** A colloidal solution in the liquid state.
- Solute** The dissolved substance in a solution.
- Solution** A dispersion in which one substance is scattered throughout another in the form of separate molecules.
- Solvent** The dissolving substance or continuous liquid portion of a solution.
- Somatic** Pertaining to the body or body cells, as contrasted with reproductive or germ cells.
- Somite** Primitive segment in the early developmental stages of higher segmental animals, persisting in the lower.
- Spectroscope** An instrument which separates light waves according to their wave lengths.
- Sperm** Male seminal fluid, containing spermatozoa.
- Spermatid** An immature sperm cell.
- Spermatocyte** An immature male germ cell during the last two meiotic divisions.
- Spermatogenesis** The maturation process of male gametes.
- Spermatozoon** The flagellated male gamete.
- Sphincter** A ring-like muscle which closes an opening.
- Spindle** The semi-solid spindle-like structure producing the central figure in cells undergoing division.
- Spirillum** A genus of bacteria characterized by spirally-twisted bodies.
- Splanchnic** Pertaining to the viscera.
- Spleen** A large ductless, gland-like organ in the abdominal cavity, active in conversion and storage of blood.
- Sporangium** A capsule in which spores are produced.
- Spore** A reproductive body, usually produced asexually, capable of growing into a new individual.
- Sporophyll** Leaf specialized for spore production.
- Sporophyte** That phase of plant reproduction which is asexual and reproduces by means of spores.
- Sporozoite** Spores formed in the life cycle of certain sporozoa, as in the malarial parasite.
- Stamen** The pollen-producing sporophyll in seed plants.

- Staminate** Pertaining to stamens or pollen producers.
- Stapes** The third ossicle of the middle ear, the stirrup.
- Staphylococcus** Spherical bacterial organisms forming irregular clusters.
- Statoblast** A multicellular asexual reproductive structure produced by bryozoans.
- Statocyst** A sense organ of equilibrium found in many invertebrates.
- Stele** The central cylinder of a vascular plant.
- Stigma** The part of the pistil which receives the pollen.
- Stoma** One of the openings in a leaf which serve in gas exchange.
- Striate cortex** The part of the cerebral cortex concerned with vision.
- Streptococcus** Spherical bacterial organism forming long chains.
- Strobilus** A specialized sporophyll-bearing branch found in some pteridophytes and spermatophytes.
- Sugar** Any one of many sweet carbohydrates, including principally monosaccharides and disaccharides.
- Sulfa drugs** A group of drugs recently found to be very effective against various microorganisms.
- Surface tension** A surface phenomenon producing the effect of a stretched elastic membrane and resulting from the attraction of molecules for each other.
- Suture** A seam or joint, as between two bones.
- Suspension** A dispersion in which the dispersed particles consist of groups of molecules.
- Swimmerets** Flattened abdominal appendages of crustaceans.
- Symbiosis** The act of two or more organisms living together in mutual dependence or advantage.
- Synapse** The juncture point of neurons in the central nervous system. The region which governs the transmission of impulses.
- Syncytium** A protoplasmic mass containing many nuclei.
- Synthesis** Building of larger molecules from smaller ones.
- Systemic** Pertaining to the body as a whole.
- Systole** The contraction phase of the heartbeat cycle.
- Tastebud** One of the specialized structures on the tongue for the discrimination of taste.
- Taxonomy** The science of classification of animals and plants.
- Tectorial membrane** Membrane projecting over the hair cells of the organs of Corti in the cochlea.
- Telophase** The end phase of mitosis.
- Tendon** Fibrous connective tissue connecting muscles to bone.
- Testis** The male gonad.
- Testosterone** The male testicular hormone maintaining secondary male sexual characteristics.
- Thallophyte** Simple thallus plant of the phylum Thallophyta.
- Thallus** The simple body of a primitive plant, not differentiated into roots, shoot, and leaves.
- Thrombin** An enzyme involved in the clotting of blood.
- Thrombus** A stationary clot of blood in a blood vessel.
- Tissue** Any united group of cells specialized to perform a similar function.
- Toxin** Any poisonous substance produced by living organisms.
- Trachea** The windpipe.
- Tracheid** Spindle-shaped conducting cells in the woody portion of wood.
- Transpiration** Loss of moisture through pores.
- Trepang** Dried sea cucumbers used as food in China.
- Trichinosis** A disease caused by the parasitic roundworm *Trichina*.
- Trichocyst** Explosive organelle in the outer protoplasm of certain ciliates thought to serve for protection.
- Triploid** Having a triple set of chromosomes instead of the usual diploid or double number.
- Tropism** A growth response of plants towards environmental stimuli.
- Trypsin** A pancreatic enzyme which splits protein into amino acids.
- Tuber** Modified shortened and thickened underground stems, such as the potato.
- Turgidity** Rigidity of a cell resulting from osmotic pressure.
- Thyroid glands** Paired glands lying in the neck region, secreting the hormone thyroxin for the control of normal growth and metabolism.
- Thyrotropic hormone** A hormone produced by the anterior pituitary gland and influencing the activity of the thyroid gland.
- Tympanic membrane** The ear drum.
- Typhlosole** The dorsal longitudinal infolding of the intestine of the earthworm.

- Umbilical* Relating to the umbilicus or navel, or the vessels which in intrauterine life lead from it to the placenta.
- Ungulates* Hoofed animals.
- Urea* The chief nitrogenous waste in urine. $\text{CO}(\text{NH}_2)_2$.
- Ureter* Duct leading from the kidneys to the urinary bladder.
- Urethra* Duct leading from the urinary bladder to the exterior.
- Uriniferous tubule* One of the convoluted kidney tubules which transport and aid in the production of urine.
- Uterus* An expanded section of the oviduct, in some animals for egg storage, in others for housing and nourishing the developing embryo.
- Utricle* The larger of two sacs of the membranous labyrinth of the inner ear, associated with the semicircular canals.
- Vacuole* A non-protoplasmic liquid bubble within the cytoplasm.
- Vagina* Female copulatory canal.
- Variation* Structural or functional differences between closely related organisms, primarily those of hereditary nature.
- Vasa efferentia* Small tortuous ducts in vertebrates leading sperm from the testis to the vas deferens.
- Vascular* Pertaining to vessels or ducts.
- Vas deferens* The primary sperm duct leading from the vasa efferentia to the ejaculatory duct.
- Vegetal pole* The pole of the egg or morula containing the greater concentration of yolk material.
- Vein* Any large blood vessel carrying blood toward the heart.
- Velamen* A layer of air-containing cells surrounding the aerial roots of certain epiphytes.
- Veliger* An advanced larval stage of most mollusks.
- Ventral* The lower or belly surface of animals.
- Ventricle* Any small cavity, as in the brain; the chamber or chambers of the heart which send blood out through the arteries.
- Vermiform appendix* A worm-shaped appendage of the caecum. The appendix.
- Vertebra* One of the bones making up the vertebral column of vertebrates.
- Villus* One of the finger shaped projections lining the inner wall of the small intestine; one of the root-like projections on the chorionic wall of the mammalian embryo.
- Virus* A living culture of pathogenic organisms; used also in reference to the filterable viruses.
- Viscera* The large internal organs of the body, especially in the abdominal cavity.
- Vitamin* An enzymatic substance essential to normal growth and metabolism.
- Viviparous* Giving birth to live young. Contrast oviparous.
- White matter* The substance of the central nervous system in cord and brain consisting of connecting nerve fibers. Contrast with gray matter.
- Wolffian duct* The mesonephric duct, later the sperm duct.
- Xerophthalmia* Dryness of the eyeball caused by a deficiency of vitamin A.
- Xylem* The inner woody portion of the vascular bundles of vascular plants.
- Yolk* Fatty food material stored in egg cells.
- Zoospore* A motile, swimming spore produced by lower plants.
- Zygospore* A zygote which assumes a resting phase after formation, as in *Spirogyra*.
- Zygote* A cell formed by the fusion of two gametes, a fertilized egg.

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